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Responses of an Endangered Songbird to an Extreme Drought Event

Melanie R. Colón^{1,2,*}, Ashley M. Long², and Michael L. Morrison¹

Abstract - Given natural variation in weather conditions and increased risk of drought associated with climate change, understanding how birds respond to fluctuations in precipitation is a necessary step toward development of more-effective, long-term management strategies for species of conservation concern. We compared behaviors and reproductive output of the federally endangered Vireo atricapilla (Black-capped Vireo, hereafter Vireo) during an extreme drought event and a year with moderate rainfall. During the drought, Vireos had lower pairing and territory success, delayed nest initiation, fewer re-nesting attempts, and lower nest-success. Brood parasitism by Molothrus ater (Brown-headed Cowbirds), which is one of the main threats to Vireo population persistence, was also greater during the drought year. Nest placement varied between years, with Vireos using the evergreen Juniperus asheii (Ashe Juniper) as a nest substrate more often when conditions were dry and the deciduous Diospyros texana (Texas Persimmon) under moderate conditions. Removal of Ashe Juniper and Brown-headed Cowbirds from Vireo habitat are common management practices used to support Vireo conservation efforts. Our results suggest that regional weather patterns should be considered when making decisions regarding Ashe Juniper removal. In addition, increased Brown-headed Cowbird removal may be warranted in dry areas during drought years.

Introduction

Although definitions vary, drought is usually characterized by inadequate precipitation over a time sufficient to impact vegetation and deplete soil moisture (Kramer 1983). Depending on drought severity, this weather phenomenon can have individual- and population-level consequences for birds. Heat waves associated with summertime droughts can result in avian mortality (McKechnie and Wolf 2010, Saunders et al. 2011), but most birds experience the effects of drought indirectly through changes in vegetation or other habitat features. For example, under drought conditions, plants may exhibit delayed phenology, reduced leaf area, or altered plant chemistry (Gutbrodt et al. 2011, Larsson and Ohmart 2008, Rathcke and Lacey 1985). Such changes in vegetation can affect the timing and abundance of available plant and insect foods (Greven et al. 2009, Morrison and Bolger 2002, Ogaya and Peñulas 2007) and reduce vegetation cover at foraging and nesting sites, thus increasing the risk of predation (Martin 1992, Sugden and Beyersbergen 1986) and exposure to the elements (e.g., wind, rain, cold, heat; Walsberg 1981).

Birds can respond to drought by relocating to wetter sites (Strong et al. 1997, Takekawa and Beissinger 2005) or by following shifting plant distributions

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(Mueller et al. 2005). Birds that remain in drought-impacted habitats may use larger areas (van Zyl 1994) or alternative nest substrates (Martin 1993) in response to reduced resource availability. Additionally, birds may delay (or forgo) breeding during drought (Christman 2002, Preston and Rotenberry 2006, Visser et al. 2006) or reduce their reproductive effort by laying smaller clutches, abandoning nests, or engaging in fewer nesting attempts (Erikstad et al. 1998). Given natural variation in weather conditions and increased risk of drought associated with climate change, understanding how birds respond to fluctuations in precipitation is a necessary step toward development of more-effective, long-term management strategies for species of conservation concern (IPCC 2014, Jiang and Yang 2012).

Vireo atricapilla Woodhouse (Black-capped Vireo; hereafter, Vireo) is a small, migratory songbird that breeds in early-successional, shrub-scrub vegetation in arid and semi-arid regions of Oklahoma, Texas, and Mexico (González-Rojas et al. 2014, Graber 1961, Grzybowski 1995). The US Fish and Wildlife Service listed the Vireo as endangered in 1987, citing habitat loss and reduced reproductive success resulting from brood parasitism as the primary threats to the species (USFWS 1987). Drought is a common occurrence across the Vireo's breeding range that helps maintain the vegetation structure needed for Vireo reproduction (Wilkins et al. 2006). However, the severity of drought conditions that occur across the Vireo's breeding range can vary widely, and Graber (1961) suggested that the impacts of drought on vegetation can cause previously occupied areas to become unsuitable for Vireos. More recently, Smith et al. (2012) noted that Vireo productivity is greatly influenced by precipitation in the dry, southwestern portion of the species' breeding range in Texas.

In 2011, Texas experienced an extreme drought event with record high temperatures and precipitation deficits (Hoerling et al. 2013). Drought persisted across the state into 2012, but it was less intense, and rainfall in many locations was comparable to long-term regional averages (NCEI 2016). The variability in precipitation between years provided a unique opportunity to examine Vireo responses to drought. Herein, we quantify differences in weather and vegetation greenness, and compare Vireo behaviors and reproductive output during the 2011 (drought) and 2012 (moderate) breeding seasons. Our results add to our understanding of Vireo breeding ecology and may help inform management and conservation efforts for this endangered species.

Field Site Description

We surveyed Vireos across an 1100-ha study site located at Dobbs Run Ranch (~29°38'60"N, 100°24'36"W) from late March–late July in 2011 and 2012. Dobbs Run Ranch is a privately owned property located in Edwards County, TX, on the southwestern edge of the Edwards Plateau (Fig. 1). Soil within the study site is predominantly limestone bedrock (99.6%; NRCS 2013), and common woody plants include *Juniper asheii* J. Buchholz (Ashe Juniper), *Quercus fusiformis* Small (Plateau Live Oak), *Pinus remota* Little (Texas Pinyon Pine), *Diospyros texana* Scheele (Texas Persimmon), and *Sophora secundiflorum* Ortega (Texas Mountain Laurel).

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Average temperature in the region during the months of Vireo breeding (April–July; Grzybowski 1995) is 31 °C, and average seasonal precipitation is ~25 cm; however, the region experiences notable variation in temperature and precipitation annually and seasonally (NCEI 2016).

Methods

Weather

2017

To quantify differences in weather between years, we obtained daily maximum temperature and daily precipitation data for 2010–2012 from the National Centers for Environmental Information (NCEI 2016). We obtained most data from the Brackettville 22 N station located at Kickapoo Caverns State Park (29°36'36"N, 100°27'07"W; Fig. 1), which is adjacent to Dobbs Run Ranch. A small number of records were missing from this station during the study period. When necessary, we substituted precipitation values from the Rocksprings 26 SSW station (29°41'16"N, 100°25'18"W; Fig. 1), 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, we substituted average values



Figure 1. Location of Dobbs Run Ranch in relation to nearby weather stations in Edwards and Kinney counties, TX. Top inset shows the study site and nest locations (solid 2011, open 2012) within Dobbs Run Ranch where we monitored Black-capped Vireos in 2011 and 2012. Bottom inset shows the location within the Black-capped Vireo's breeding range in Texas (gray shading).

from the next 2 nearest stations (Carta Valley $[29^{\circ}47'24"N, 100^{\circ}40'26"W]$ and Brackettville $[29^{\circ}18'58"N, 100^{\circ} 24'50"W]$; Fig. 1), which were both located <30 km away. Substitutions accounted for <5% of weather data.

Greenness

To quantify vegetation greenness, we used ENVI software v. 5.1 and 5.2 (Exelis Visual Information Solutions, Bouder, CO) to create normalized difference vegetation index (NDVI) maps from 30-m resolution Landsat images taken in April and May of each year. We then used the Spatial Analyst extension in ArcMap v. 10.2.2 (Environmental Research Systems Institute, Redlands, CA) 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; Cihlar et al. 1991, Nicholson et al. 1990).

Territory and nest surveys

Each year from 20 March to 15 July, we conducted auditory and visual surveys across the study site to locate male Vireos. We marked the locations of all males with handheld Garmin RINO 120 GPS units (≤ 10 m accuracy). We returned to marked locations every 5–10 d between the hours of sunrise and 1400 to define territory boundaries and determine mating and reproductive status. Each time a focal bird moved ≥ 20 m, we recorded its location with a GPS. To improve our assignment of individuals to specific territories, we used standard target mistnetting techniques with playback of recorded Vireo song to capture adult Vireos, which we then banded with unique color-band combinations. We considered males territorial if they occupied the same locations for ≥ 4 weeks, and we considered territorial males paired if we consistently observed them with females or they maintained active nests.

To locate nests, we observed the movements of Vireos engaged in behaviors indicative of breeding (e.g., copulation, material or food carry, presence of fledglings). We focused on females because they tend to spend more time near nests (Grzybowski 1995, Pope et al. 2013b), but we also noted male behaviors and movement patterns because this species shares parental duties (Grzybowski 1995, Pope et al. 2013b). If we did not detect Vireos on arrival in a territory, we systematically searched the area for nests (Bailey and Thompson 2007, Smith 2011). This method often proved effective in the absence of behavioral cues—especially during the egg-laying phase when nests were most difficult to find (e.g., Martin and Geupel 1993)—and accounted for differences in detection attributed to variation in vegetation. We monitored Vireo nests every 2–3 days until they fledged young, failed, or were abandoned, and recorded adult behaviors and nest contents on each visit. We banded all Vireo nestlings aged 6–8 d with unique color-band combinations.

We did not remove (or addle) *Molothrus ater* Boddaert (Brown-headed Cowbird; hereafter Cowbird) eggs from parasitized nests because their presence can deter future parasitism (Ortega et al. 1994), but we removed all Cowbird nestlings on discovery. Parasitized Vireo nests rarely fledge host young (Boves et al. 2014, Grzybowski 1995, Tazik 1991), and by dispatching Cowbird nestlings before they fledged, Vireos did not engage in post-fledging care of non-host young, increasing their opportunities to re-nest. We considered a parasitized nest as failed for the purposes of our analyses (see below) if it contained Cowbird nestlings at any point. We considered a nest successful if it fledged ≥ 1 Vireo young, provided we did not previously dispatch any Cowbird nestlings. Young Vireos remain with their parents for 2 or more weeks before independence (Grzybowski 1995); therefore, we surveyed all territories in which we suspected fledging for a minimum of 2 weeks after the expected fledging date. If we detected a fledgling (≤ 2 weeks of age) within the territory, we recorded the territory and the nest as successful. We also considered territories and nests successful if 2 or more observers independently identified a banded fledgling, regardless of fledgling age or location within the study site.

We catalogued vegetation characteristics for each active (i.e., eggs or nestlings tended by adults) Vireo nest after it fledged, failed, or was abandoned. Specifically, we recorded the nest substrate to the nearest 0.1 m and measured the distance to the nearest edge (i.e., nest rim to nearest leafy edge), nest height (from ground to nest rim), nest substrate height, and canopy height. In addition, we positioned a 2-m coverboard marked with 0.1-m² 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 (Guthrey et al. 1981). We averaged these values to obtain a single measurement of foliage cover. Lastly, we placed a 0.1-m² 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 1 m above and 1 m below (where possible). We 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; Pope et al. 2013a, 2013b; Smith et al. 2012).

Data analyses

We conducted all tests using the statistical program R v. 3.2.2 (R Core Team, Vienna, Austria). We present all means described below with their associated standard deviations. Our intent was to examine Vireo responses in relation to specific weather characteristics. However, our analyses indicated clear differences in our weather and greenness metrics between 2011 and 2012 (see below). As such, we simplified our analyses by using temporal variables (i.e., day, year) as proxies to examine Vireo responses to weather.

Weather. We calculated the mean maximum daily temperature for each year and used a Welch's 2-sample *t*-test (Crawley 2014:94–95, Ruxton 2006) with Cohen's *d* as a measure of effect size (Lakens 2013) to compare means between years. We also used linear regression to examine temperature as a function of date within seasons (Crawley 2014:114–140). We summed daily precipitation to determine cumulative monthly precipitation totals for the 7 months leading up to and the 4 months of each Vireo breeding season, and calculated the percent differences in seasonal rainfall between years.

Greenness. We calculated the mean NDVI of all pixels across the study site to determine mean NDVI on the landscape for each year. We also calculated the mean NDVI for each territory and used those values to determine the annual mean NDVI for all territories. We compared NDVI on the landscape as well as mean NDVI within territories between months and years using 2-way factorial analysis of variance tests (ANOVA; Crawley 2014:170–173). If there was a significant interaction between month and year, we used Tukey's honest significant difference (HSD) tests 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, we examined the main effects of month and year separately.

Territories and nests. We used Geospatial Modelling Environment v. 0.7.3.0 (Beyer 2009) to create minimum convex polygons (MCP) for all territorial males with ≥ 15 location points, which we considered the minimum number required to adequately represent territory boundaries (e.g., Morgan 2012, Smith 2011). We defined territory size as the area within each MCP and compared territory size between years using a Welch's 2-sample *t*-test (Crawley 2014:94–95, Ruxton 2006) with Cohen's *d* as a measure of effect size (Lakens 2013). We calculated pairing success as the number of paired males relative to the total number of territorial males (Long et al. 2017, Stewart et al. 2014). We calculated territory success as the number of successful territories relative to the total number of paired males (Long et al. 2017, Stewart et al. 2014). We examined inter-annual differences in pairing and territory success using Fisher's exact tests (Crawley 2014:105–107) and calculated the odds ratios (OR) as measures of effect size (McHugh 2009).

We used a chi-square test with Cramer's V as a measure of effect size to determine if nest substrate use differed between years (Crawley 2014:101–105), and we used a 1-way, non-parametric, ANOVA-type multivariate test (reviewed in Bathke et al. 2008) 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 4 most common nest substrates (i.e., global models). We subsequently used post hoc univariate tests to examine each vegetation characteristic across years and substrates. We accounted for multiple comparisons in post hoc tests using the Bonferroni correction and interpreted Pvalues accordingly. We also examined the relative effects for each test. Relative effects are measures of effect size that 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).

We 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, we calculated the mean initiation date for each year and examined annual differences using a Welch's 2-sample *t*-test (Crawley 2014:94–95, Ruxton 2006) with Cohen's *d* as a measure of effect size (Lakens 2013). We 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).

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We calculated mean clutch and brood sizes of nests for each year, excluding nests from analyses for which these metrics could not be determined. We used a 1-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 Vireo clutch size declines over the season (Campomizzi et al. 2013, Graber 1961, Locatelli et al. 2016). We used a chi-square test (Crawley 2014:101–105) with phi (φ) as a measure of effect size (Hojat and Zu 2004) to compare hatching success between years, then used ANCOVA (Tabachnick and Fidel 2006:20) to examine the effect of year on brood size while controlling for clutch size. We excluded parasitized nests from analyses of clutch and brood size because Cowbirds may remove eggs or young from nests (Conkling et al. 2012, Peer and Bollinger 2012, Sealy 1992). We calculated eta-squared (η^2) as a measure of effect size for both ANCOVA tests (Maher et al. 2013).

We used Fisher's exact tests (Crawley 2014:105–107) with odds ratios (McHugh 2009) to examine inter-annual differences in the frequency of nest abandonment and brood parasitism. In addition, we developed a priori models that included year and nest vegetation characteristics to examine their effects on nest success. We used a generalized linear model approach to determine which models best predicted nest success. Models included null, main effects, and additive models for year and each vegetation characteristic. We also examined additive models with nest substrate and each of the other vegetation characteristics with year as a covariate. To test whether use of the dominant substrate in either year contributed to nest success, we coded nest substrate as a binary variable with 1 = the dominant substrate in a given year, and 0 = all other substrates. Nest substrate was correlated with distance to edge (r = -0.16, P = 0.03) and nest-substrate height (r = 0.23, $P \le 0.01$). As such, we excluded additive models that included nest substrate and these metrics from the final model set.

We also examined a priori models of daily nest survival that included year, parasitism, nest stage, 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, we considered the first day of each season to coincide with the earliest nest initiation date in that year. We used the logisticexposure method described by Shaffer (2004) to estimate daily nest survival. We included abandoned nests—which we considered as failed during the interval that abandonment was first suspected—as well as nests that contained Cowbird eggs, which we considered failed during the interval in which any Cowbird eggs hatched. As described above, we excluded nests that contained Cowbird nestlings when initially located because we considered these failed on discovery. The final model set included a null model, main effects models for each variable, and additive models with combinations of these variables. We ranked models of nest success and daily nest survival using Akaike's information criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002:49–97). We considered all models with ΔAIC_c < 2.0 to be equally possible, but identified the most parsimonious of these models as the most plausible.

Results

Weather

Mean maximum daily temperature was 34 ± 4 °C (variation = 20–39 °C) in 2011 and 32 ± 4 °C (variation = 17–40 °C) in 2012. Maximum daily temperature varied between years ($t_{241.4} = 4.85$, $P \le 0.01$, d = 0.62), and daily maximum temperature increased over time within years (2011: $F_{1, 120} = 59.66$, $P \le 0.01$, $r^2 = 0.33$; 2012: $F_{1, 120} = 80.78$, $P \le 0.01$, $r^2 = 0.40$). There was 54% less rainfall in the 7 months leading up to the 2011 breeding season (13.1 cm) than during the corresponding months the following year (28.4 cm). Similarly, 56% less rain fell during the 2011 breeding season (10.7 cm) than during the 2012 season (24.5 cm). Cumulative rainfall during the 2012 breeding season was similar to the long-term seasonal average for the region, while cumulative rainfall during the 2011 breeding season was approximately half the long-term seasonal average (NCEI 2016). However, cumulative precipitation totals belie the true conditions of the 2011 breeding season during which 61% (6.48 cm) of the total rainfall occurred on a single day (12 May), and mean precipitation of all other rainfall events (n = 7) was low (0.61 ± 0.44 cm).

Greenness

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

Territories and nests

We mapped and monitored 148 Vireo territories in 2011 and 132 Vireo territories in 2012. Overall mean territory size was 1.69 ± 0.95 ha, with no significant difference in territory size between years ($t_{265.24} = -0.09$, P = 0.93, d = 0.01). The percentage of territorial males that successfully paired varied significantly between years with 82% (n = 121) successfully pairing in 2011 and 99% (n = 130) in 2012 (Fisher's exact test $P \le 0.01$, OR = 14.40). Similarly, the number of paired males with successful territories also varied by year, with 11% (n = 13) in 2011 and 78% (n = 102) in 2012 (Fisher's exact test $P \le 0.01$, OR = 29.66).

Table 1. Mean (and standard deviation) NDVI across the landscape and within Black-capped Vireo territories at Dobbs Run Ranch, Edwards County, TX, in 2011 and 2012.

	2	2011		2012		
NDVI	April	May	April	May		
Landscape	0.35 (0.06)	0.29 (0.03)	0.36 (0.04)	0.37 (0.05)		
Territory	0.28 (0.03)	0.29 (0.02)	0.37 (0.03)	0.38 (0.04)		

We located and monitored 74 active nests in 2011 and 112 active nests in 2012 (Fig. 1). Vireos placed nests in 8 plant substrates including: Texas Persimmon (n = 69), Ashe Juniper (n = 63), Plateau Live Oak (n = 25), Forestiera reticualta Torr. (Net-leaf Forestiera; n = 14), Quercus sinuata Walter var. breviloba (Torr.) C.H. Mull (White Shin Oak; n = 6), Mahonia trifoliolata (Moric.) Fedde (Agarita; n = 4), Texas Mountain Laurel (n = 3), and Karwinskia humboldtiana (Schult.) Zucc. (Coyotillo; n = 1). We found a significant difference in nest substrate use between years ($\chi^2_7 = 75.41$, $P \le 0.01$, V = 0.64). In 2011, Vireos placed 64% (n = 47) of nests in Ashe Juniper compared with only 15% (n = 16) in 2012. Texas Persimmon was the most common nest substrate in 2012, accounting for 58% (n = 65) of nests compared to only 5% (n = 4) the previous year. Vireos did not place nests in Netleaf Forestiera in 2011 or in Coyotillo or White Shin Oak in 2012. Vireos placed nests in all other substrates similarly across years.

The global model comparing vegetation metrics at nest sites across years was not significant ($F_{4.97, 875.27} = 1.96$, P = 0.08). The relative effects indicated a >50% probability that overstory height, distance to edge, average cover, and average concealment may have been greater at nests in 2012 compared with randomly selected nests from either year; however, univariate post hoc tests showed no annual differences in these or other characteristics. The global model comparing vegetation characteristics among the 4 most-common nest substrates was significant ($F_{15.54, 555.71} = 4.20$, $P \le 0.0001$). Univariate post hoc tests, however, suggested the only difference was in nest substrate height ($F_{3.00, 107.26} = 15.37$, $P \le 0.0001$), 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 (Fig. 2).

We determined the earliest nest initiation dates were 18 April in 2011 and 1 April in 2012. Mean nest initiation date overall was 9–10 May \pm 19 days, but variation in the timing of breeding was significantly different between years ($t_{153.96} = 3.45$, P < 0.01, d = 0.56). Vireos laid clutches an average of 11 days later in 2011 than in 2012 (2011: mean = 16 May \pm 14 d, 2012: mean = 5 May \pm 23 d). It should be noted that later breeding in 2011 was not a function of later arrival on the breeding grounds because Vireos arrived in similar numbers in both years starting in late March (M.R. Colón, pers. observ.). The mean initiation dates of the earliest 20% of nests were 25 April 2011 and 11 April 2012. 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.

Vireos often re-nest after failed nesting attempts or lay a second clutch after successful attempts (Grzybowski 1995); thus, mean nest initiation dates alone may not accurately reflect differences in the timing of breeding between years. To better demonstrate inter-annual differences, we graphed nest initiation dates by year (Fig. 3). In 2012, nest initiation date had a bimodal distribution, with the second peak likely corresponding with re-nesting or second brood attempts. However, because many nests are not found (Mayfield 1975), it is not always possible to determine the number of nesting attempts made per pair. That said, in some instances,

we were able to confirm re-nesting attempts because males were banded or because of male behavior and the location of nests within territories. We confirmed that 3 nests in 2011 and 19 nests in 2012 were re-nesting attempts following prior nest failure, and 7 nests in 2012 were attempts to produce a second brood after an earlier nest fledged.

Overall clutch size varied from 2 to 4 eggs (mean = 3.75 ± 0.47 eggs, n = 128 nests). Proportionally, there were more 3-egg clutches in 2011 than in 2012 ($F_{1,110} = 5.62$, P = 0.02), but after controlling for nest initiation date, we found no effect of year on clutch size ($F_{1,109} = 2.57$, 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 ($\chi^2_1 = 3.14$, P = 0.08, $\varphi = 0.14$). Overall brood size ranged from



Figure 2. Boxplot comparing nest substrate height at Black-capped Vireo nests within the 4 most commonly used nest substrates at Dobbs Run Ranch, Edwards County, TX, in 2011 and 2012. Boxes represent the middle (50%) range of substrate heights, with the thicker black lines indicating median substrate heights. Lines extending above and below each box identify the full range of substrate heights, with black dots representing outliers.

1 to 4 young with a mean of 3.48 ± 0.79 young. After controlling for clutch size, we found 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 between years.

Vireos abandoned 9% (n = 7) of nests in 2011 and 6% (n = 7) of nests in 2012 (Fisher's exact test P = 0.57, OR = 1.56). 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 Cowbirds parasitized nests, but we only found 2 nests that were parasitized before mid-May. Apparent nest success was 15% in 2011 and 41% in 2012. The additive effects of year, nest substrate, and average concealment best predicted overall nest success (Table 2). The predicted probability of nest success was higher in 2012 and increased with increasing nest concealment. In both years, Vireo nest success was lower for nests placed in the most commonly used substrate; however, overlapping confidence intervals suggest that differences associated with nest substrate were not statistically



Figure 3. Density plot showing initiation dates (Julian) of Black-capped Vireo nests within the study site at Dobbs Run Ranch, Edwards County, TX, in 2011 and 2012.

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or biologically significant (Fig.4). The top 2 models that best predicted daily nest survival included year and quadratic day trends, and one also included nest stage (Table 2). Daily nest survival was lower in 2011 and decreased over time within seasons. Survival was also lower during the nestling stage than during egg stage (i.e., egg laying and incubation). According to the most parsimonious model, mean predicted daily nest survival was 93% (\pm 3%) in 2011 and 95% (\pm 4%) in 2012.

Discussion

Weather conditions at our study site were substantially different between years. The 2011 Vireo breeding season was warmer and drier than the 2012 season. In the drier year, Vireos paired less frequently, used alternative nest-substrates, delayed nest initiation, and had lower territory and nest success. Our results are similar to observations from the drier, western portion of the species' breeding range in Texas (Graber 1961, Smith 2011, Smith et al. 2012); however, reports from the wetter, eastern parts of the range suggest the impacts of drought

Table 2. Top 10 models for hypotheses of Black-capped Vireo nest success and daily nest survival at Dobbs Run Ranch in Edwards County, TX, in 2011 and 2012. Model variables: nest substrate = dominant species (yes or no); average concealment = average vegetation cover within 1 m; overstory height = height of tallest woody vegetation above nest; nest height = height from ground to nest rim; average cover = average vegetation cover within 7 m; substrate height = height of nest tree or shrub; day = day of season; nest stage = egg or nestling; parasitism = nests parasitized by Brown-headed Cowbirds. Statistics presented: K = number of parameters in the model; LL = log likelihood; AIC_c = Akaike's information criterion for small sample sizes; ΔAIC_c = difference in AIC_c; w = Akaike weight.

Response/model	Κ	LL	AIC_{c}	ΔAIC_c	W
Nest success					
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
Daily nest survival					
Year + day^2 + nest stage	4	-349.72	708.18	0.00	0.46
Year + day	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^2 + 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 ²	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

may vary regionally according to the precipitation gradient. For example, Cimprich and Heimbuch (2011, 2012) monitored Vireos at Fort Hood during the same years as our study. Although they observed significantly more re-nesting and second brood attempts in 2012, they found that Vireo pairing, territory, and nest success were relatively similar in both years.

Statewide, the period from October 2010 to September 2011 was the driest consecutive 12-mo period in recorded Texas history (Hoerling et al. 2013). Given that precipitation is the main driver of aboveground primary productivity (Noy-Meir 1973, Sala et al. 1998), it is not surprising that we observed significantly lower vegetation greenness in 2011 compared to 2012. Food availability is often directly related to precipitation and vegetation greenness (Greven et al. 2009, Morrison and Bolger 2002, Ogaya and Peñulas 2007), and birds may use vegetation as a cue for future food availability (Marshall and Cooper 2004), defending larger or smaller territories accordingly (Orians 1961, Pitelka et al. 1993, Smith and Shugart 1987). We found no difference in Vireo territory size across years, perhaps because the costs associated with defending larger territories were greater than the benefits of securing additional resources or because Vireos compensated for any food limitation in other ways (e.g., delayed nest initiation).

Nest-site characteristics varied little between years, with the notable exception of nest substrate. There was pronounced variation in nest substrate use between years, with a majority of Vireos selecting Ashe Juniper in 2011 and Texas Persimmon in 2012. Bailey and Thompson (2007) previously suggested that Vireos were considerably less likely to place nests in Ashe Juniper compared with deciduous trees and shrubs. However, Ashe Juniper is a drought-tolerant evergreen species



Figure 4. Predicted probability of Black-capped Vireo nest success (with 95% confidence intervals) as a function of nest concealment and use of common nest substrate at Dobbs Run Ranch, Edwards County, TX, in 2011 and 2012. Nests placed in the most common nest substrate (Ashe Juniper in 2011 and Texas Persimmon in 2012) are coded "yes", and nests in all others substrates are coded "no". Gray shaded areas indicate confidence intervals.

(Gilman and Watson 1993) that can access deep water sources when surface soils are dry (Jackson 1999). At our study site, Ashe Juniper was one of few species with consistently green foliage in 2011 (M.R. Colón, pers. observ.), and it may have provided cover at nest sites when deciduous species were bare. This hypothesis is supported by our analyses of nest-site vegetation, which demonstrated that Vireos were able to locate nest sites with similar characteristics (e.g., concealment) across years despite the differences in vegetation greenness and nest substrate use.

Nonetheless, Vireos had lower reproductive success during the drought year, some of which may have resulted from differences in 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 (Bourgault et al. 2010, Farner and Follett 1979, Marshall and Cooper 2004), and timing reproductive activities with rainfall is a common behavioral strategy for birds inhabiting arid regions (e.g., Lloyd 1999, Ohmart 1969, Zann et al. 1995). The mean nest initia-tion date for Vireos at our study site in 2011 (16 May) was within a few days of the single greatest day of rainfall that season (12 May), suggesting that, as with other species, rainfall may have stimulated breeding activity in Vireos that year.

Delayed nest initiation may be adaptive when resources are limited; however, there are still consequences for annual fecundity. For example, clutch size declines seasonally in many species (Drent and Daan 1980, Klomp 1970, Martin 1987). In our study, we found no difference in clutch size between years after accounting for nest initiation date, but birds that nested later in the season laid fewer eggs than those that nested earlier. Similarly, annual fecundity may be determined by the number of nest-ing attempts in a season. In 2011, later nest initiation at our study site corresponded to a shortened breeding season that year, and we observed fewer re-nesting attempts and no second brood attempts. Additionally, snakes and Cowbirds, common nest predators at Vireo nests (Conkling et al. 2012, Stake and Cimprich), are more active later in the Vireo breeding season (e.g., Boves et al. 2014, Sperry et al. 2008). Cowbirds present the added risk of nest failure from brood parasitism. Birds that delay nesting increase their exposure to snakes and Cowbirds, which may explain the lower territory and nest success and higher parasitism rates we observed in 2011.

Our results represent only a snapshot of the potential impacts of drought on Vireos, and longer-term studies are needed to understand how population persistence might be affected under prolonged or more frequent drought events. Drought has been common throughout the Vireo's breeding range for over 1000 years (Cleaveland et al. 2011, Toomey et al. 1993, USDM 2016), but statewide climate models predict that temperatures will steadily increase in Texas through the 21st century, with warmer weather corresponding to drier conditions (Jiang and Yang 2012). Although it is not possible to control such events, wildlife managers can plan for their inevitability by understanding the responses of species of conservation concern and identifying ways to minimize the consequences.

Current management recommendations for Vireos include the removal of Ashe Juniper and Cowbirds from Vireo habitat (Campbell 1995). However, Grzybowski

et al. (1994) suggested that Ashe Juniper may provide important cover in areas where deciduous vegetation is limited, especially in the drier, western portion of the species' breeding range in Texas. More frequent use of Ashe Juniper by Vireos at our study site during the drought year suggests that Ashe Juniper may also be important when deciduous vegetation is stressed. As such, regional weather patterns as well as vegetation composition should be considered when making decisions regarding Ashe Juniper removal in Vireo habitat. Additionally, 20% of Vireo nests at our study site were parasitized by Cowbirds during the drought year. Managers typically try to limit Cowbird parasitism of Vireo nests to <10% annually (e.g., Kostecke et al. 2005, USFWS 2000). Our results suggest that increased Cowbird removal during drought years may be advisable. According to Summers et al. (2006), Cowbird trapping is most effective in March and April before Cowbirds become reproductively active and less effective in May when most nest parasitism occurs. Locally breeding Cowbirds may be less attracted to grain-baited traps in May because they switch to an insectivorous diet once they become reproductively active (Ankney and Scott 1980). However, if insect abundance is lower during drought years, continued trapping during May might be beneficial alone or in combination with other management actions (S.G. Summers, US Army Natural Resources Management, Fort Hood Military Reservation, Killeen, TX, pers. comm.), though results are likely to vary with regional aridity.

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