THE INFLUENCE OF NEST SITE CHARACTERISTICS ON NEST SUCCESS AND

PARASITISM OF BLACK-CAPPED VIREOS (*VIREO ATRICAPILLA*) IN THE

SOUTHWESTERN EDWARDS PLATEAU

by

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LIST OF ABBREVIATIONS

Abbreviation	Description
AIC	Akaike Information Criterion
ΔAIC	Difference in AIC units between the top model and specified model that is used in model selection
BCVI	Black-capped Vireo
BHCO	Brown-headed Cowbird
DSR	Daily survival rate
IUCN	International Union for Conservation of Nature
USFWS	United States Fish and Wildlife Service
TPWD	Texas Parks and Wildlife Department

ABSTRACT

The Black-capped Vireo (*Vireo atricapilla*) was delisted from the U.S. Endangered Species List by the United States Fish and Wildlife Service (USFWS) in 2018. As part of the USFWS Post-Delisting Monitoring Plan, nest searching and monitoring of vireo nests were completed in 2021 and 2022 to provide an estimate on parasitism and nest success in the region. Field work for this study took place in Kickapoo Cavern State Park in the western Edwards Plateau of Texas. The two field seasons were characterized by mild drought conditions in 2021 and exceptional drought conditions in 2022. The logistic exposure method was used to quantify the relative success vireo nests had in each year. Nests found in 2021(n = 18) had a daily survival rate (DSR) of 0.96 and an overall chance of survival from nest building to fledging of 40.5%. Nests found in 2022 (n = 15) had a DSR of 0.88 and an annual survival rate of 4.6%. Additionally, in 2021 vireos only nested in Ashe Juniper (*Juniperus ashei*) 16% (n = 3) of the time while in 2022 juniper was utilized in 46% (n = 7) of nests. This is of particular importance because juniper removal is one method used to help enhance potential Black-capped Vireo habitat. Black-capped Vireo nests were parasitized by Brown-headed Cowbirds 33% (n = 6) and 47% (n = 7) of the time in 2021 and 2022, respectively. The results of this study will help inform management decisions for Black-capped Vireo populations as historic drought conditions likely become more common under changing global climates.

I. THE INFLUENCE OF VARIED-SCALE CHARACTERISTICS ON BLACK-CAPPED VIREO (*VIREO ATRICAPILLA*) NEST SUCCESS IN THE SOUTHWESTERN EDWARDS PLATEAU

Introduction

The Black-capped Vireo (*Vireo atricapilla*) is a small songbird that has been the focus of research and conservation over the past several decades. Restricted to breeding in a narrow range of North America known for its hot climate, this bird can be found in areas of Oklahoma, North, Central, and West Texas southwards into northern Mexico, occupying low scrubby deciduous vegetation (Grzybowski 2020). Researchers have found active nests in Nuevo León and Tamaulipas, Mexico, which indicate that the breeding range for this species has extended farther south of the previously known extent (Gonzalez-Rojas et al. 2013). While never being a bird that had a very large breeding range, the species historically stretched into central Kansas before early declines were noted (Graber 1961). Threats from nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) and habitat loss and degradation, including urbanization and wildfire suppression, have been linked to the decline of this species and why it was ultimately designated as threatened in 1987 under the U.S. Endangered Species Act (Grzybowski 2020). Additionally, habitat loss due to the impacts of historic and active overgrazing on the near-ground vegetation cover also negatively affects the habitat for Vireos (Grzybowski et al. 1986). While the Black-capped Vireo has been well studied in the eastern area of their breeding range, there remain some knowledge gaps about the species within the western limit, including certain nest site characteristics, nest success, and parasitism rates. Some notable research of western populations includes works by Colon et al. (2017) and Smith-Hicks et al. (2017).

Black-capped Vireos build their nests at or near the terminal fork of branches in deciduous shrubs, usually between 0.5–2.0 meters in height (Grzybowski et al. 1986). The cup-shaped nests are normally found hanging over the internal open spaces of the nest substrate but occasionally can be found hanging in the open space between two bushes (Grzybowski 2020). While not the primary choice, junipers can be tolerated by the birds as a nesting substrate when they are found in the normal, patchy habitat configuration rather than a thick forest (Grzybowski et al. 1986).

Because many other members of the Vireonidae family, like the Black-capped Vireo, share high parasitism rates by Brown-headed Cowbirds, it is important to consider nest placement towards the edge of the nest substrate which may lead to the nest to being easier to find (Bent 1965). A study on Gray Vireos (*Vireo vicinior*) found that nest survival was related to nest placement and foliage density, with nests being placed closer to the center of a tree with low foliage density having higher likelihood of survival (Harris et al. 2021). It has been found that habitat attributes differ between nests that are predated by birds versus those that are predated by mammals due to differences in search strategies (Liebezeit and George 2002). Additionally, researchers at Fort Hood found that Black-capped Vireo nests that were placed on the inside of the nest patch were parasitized more often than those on the edge (Sibole and Green 2009). This is important and relevant for this study as Black-capped Vireos are exposed to a large mix of all types of predators (avian, mammalian, reptilian) and therefore nest height for Black-capped Vireos may differentially influence predator access to the nest.

Another important characteristic of nest site selection that is sometimes overlooked is soil type because the plants that grow, and ultimately form the nest

substrate, are directly tied to the soil they grow in. Nesting habitat is usually localized for Black-capped Vireos because the plant communities are generally maintained in edaphic settings found in places like rocky gullies, edges of ravines, and eroded slopes (Grzybowski 2020). Additionally, the Cretaceous limestones found in Texas underly shallow soils that host plant species and spatial heterogeneity that is important for typical Black-capped Vireo nesting habitat (Grzybowski et al. 1994).

Due to the need for successional habitat in which to breed, disturbance and management are important for maintaining sufficient breeding habitat for future generations (Graber 1961). However, it is important to note that these disturbances can vary across the breeding range. Some areas of the Edwards Plateau have maintained this habitat with many years of periodic wildfires while other areas of the Edwards Plateau have been disturbed through heavy goat grazing and bulldozing, respectively (Grzybowski et al. 1994). It is also worth noting that in some cases junipers contribute as important cover where deciduous vegetation is lacking, as in areas of the Edwards Plateau and to the southwest (Grzybowski et al. 1994). The specific objective I have addressed by performing this 2-year study was to investigate how various temporal and environmental characteristics around the nest influence nesting success.

Methods

<u>Species Description</u>

The Black-capped Vireo (*Vireo atricapilla*) is a foliage gleaning songbird belonging to the family Vireonidae that breeds from Oklahoma through central and southwestern Texas and into northern Mexico. Black-capped Vireos are unique among vireos by being sexually dichromatic to humans viewing them in the field (Grzybowski

2020). Males have a dark black cap that forms spectacles around the eyes while females and immature males have a similar cap that is a duller gray than mature males. Major threats to their population include Brown-headed Cowbird brood parasitism and loss of breeding habitat through destruction or natural successional changes (Grzybowski 2020). After being placed on the Endangered Species List in 1987, the species has been recovering and recent surveys between 2009 and 2014 have shown the population had grown to 5,244 adult males (United States Fish and Wildlife Service [USFWS] 2018). With the recent growth in population, the species was removed from the U.S. Endangered Species List but remains of conservation concern and is listed as near threatened by the IUCN Red List (2021).

The species prefers to nest in areas with low-growing, shrubby mottes of vegetation with spaces and openings within the vegetation that is generally either early successional or in edaphic settings like gullies, ravines, and slopes (Graber 1961, Grzybowski 2020). In the Edwards Plateau the vireos are found in areas of deciduous scrubland with vegetation ranging in height from 0–2 meters (Grzybowski et al. 1994). While its range is rather small, there is a large variety of plant species that provide ideal habitat for the Black-capped Vireo. Some of the plant species most frequently encountered across the breeding range are species of oaks (*Quercus* spp.), sumacs (*Rhus* spp.), Texas persimmon (*Diospyros texana*), roughleaf dogwood (*Cornus drummondii*), and redbud (*Cercis canadensis*) (Graber 1957, Tazik et al. 1993, Benson and Benson 1990, Grzybowski et al. 1994, Grzybowski 2020). In Texas, this type of vegetation is commonly found in areas with Fredericksburg limestone that supports poor soils (Grzybowski 2020). Other areas of the breeding range, Oklahoma and Mexico, contain

different species of vegetation that the vireos have been found to nest in including

blackjack oak (*Q. marilandica*), post oak (*Q. stellata*), madrone (*Arbutus xalapensis*),

lantrisco (*Rhus pachyrrachis*), orchid tree *(Bauhinia ramossisima)*, and thickleaf

milkberry (*Chiococca pachyphylla*) (Graber 1961, Gonzalez-Rojas et al. 2014).

Study Site

Kickapoo Cavern State Park is a 2,577 hectare (6,368 acre) state park owned and

operated by Texas Parks and Wildlife Department (TPWD) that lies north of

Brackettville, Texas, straddling the Kinney/Edwards County line. Before being acquired

by TPWD in 1986, the land was owned by the Seargeant Ranch. The park is

characterized by a mosaic of vegetation from three different natural regions of Texas

including live oak-juniper woodlands of the Edwards Plateau, thorny shrubs of the South

Texas Brush Country, and cacti of the Trans Pecos (Texas Parks and Wildlife Department

2020). The wide variety of vegetation allows for a large number of bird species to inhabit

the park as both migrants and residents, including the Golden-cheeked Warbler and

Black-capped Vireo. Kickapoo Cavern State Park is listed as "Manageable" with 64

males at the last official census of Black-capped Vireos for the park, per the Post

Delisting Monitoring Plan (USFWS 2018).

Survey Protocol

I assessed nest success and parasitism rates by using a nest searching and

monitoring protocol. Nest searching and monitoring occurred from the beginning of May

until the middle of July of 2021 and 2022. Nests were found by following standard nest

searching and monitoring protocols outlined by Martin and Geupel (1993) and

monitoring for nesting behavior such as singing males, courting behavior, and birds with

food or nesting material in their mouths. Locations that were found to have any of the listed activities, but did not result in finding a nest, were recorded and searched at a later date because these behaviors indicated a nest was likely present and extended human activity could cause nest abandonment or depredation.

At each nest, I recorded nest substrate, nest height, orientation of nest, and the date it was located. GPS coordinates for the nest were recorded both manually (e.g., data sheet) as well as on electronic devices (e.g., Garmin GPS and the ArcGIS Collector app). Flagging tape was placed on a nearby tree to further facilitate re-locating nests. A compass direction was taken from the flag facing towards the nest, with a distance estimation from the flag to the nest, both recorded on the data sheet.

Once located, nests were monitored every 3–5 days as conditions permitted (USFWS 2018). Nest checks were conducted by nest pole camera (e.g., smartphone attached to selfie stick) so nest contents could be observed away from the nest. This method helped minimize disturbance to the nest, as well as prevented leaving a scent to attract mammalian predators or drawing the attention of avian predators from parental alarm calls. At each nest check, including the first time a nest is found, I recorded the date of the check, number of eggs in the nest (both BCVI and BHCO if present), and number of nestlings (both BCVI and BHCO if present and at that stage). Notes were taken at each check for anything significant that happened. Examples of significant events at the nest included evidence of nest building, flushing a bird off the nest, or evidence of predation upon discovering a failed nest.

Finally, I determined nest fate (i.e., success or failure) based on evidence at and around the nest. Nest success was defined as evidence of fledglings (begging, parents

feeding, etc.) present at or near the nest. Nest failure was determined based on nest contents and potential signs in and around the nest. I assumed that if a nest was empty upon that check and the nest was either still at the incubation stage or too early for fledging, then the nest had been depredated. I assumed that a nest had been abandoned causing failure if there was no parental activity around the nest for consecutive checks, equaling about a week in time.

Statistical Analyses

All statistical analyses were completed using the statistical program R version 4.2.1 (R Core Team, Vienna, Austria). I created *a priori* models to evaluate the influence of different covariates and their interactions on daily survival rate. Some covariates were on a temporal scale (Year, Julian date of discovery), while others were at the nest-site scale (Nest substrate, Nest height).

Nest Success – Daily survival rates were calculated using the logistic exposure method for calculating nest success as laid out by Shaffer (2004) and Rotella et al. (2004). Annual survival was calculated by taking the average daily survival rate for each year and raising that value to the length of time for a full nesting cycle, in the case of Black-capped Vireos, that value is 25 (Gryzbowski 2020). The global model was used to calculate the daily survival rates in the first generalized linear model. Once the daily survival rate was calculated for each nest, it was used as the response variable to assess the fit of the models using an information theoretic approach (Burnham and Anderson 2002). Models were selected using Akaike Information Criterion (AIC) where the lowest

AIC was the selected model when there were no competing models. Competing models were those with ΔAIC ≤ 2 and in this case, the most parsimonious model was selected.

Results

In 2021, a total of 22 nests were found and monitored. However, four of these nests were located and found to be empty after following parents and fledglings. These four nests were omitted from analysis because we were not able to observe activity from any stage of development in the nest. The 2022 season resulted in a total of only 16 nests being found. Thirteen of these nests failed, two were abandoned before eggs could be laid, and one was located empty but investigation of the area resulted in seeing fledglings being fed by a male. The empty nest that was located was omitted from analysis because I was not able to observe activity from any stage of development in the nest. Nests found in both years were all found in similar areas of the park, representative of more open, shrubby habitat rather than dominated by thick juniper forests (**Figure 1**).

Nest substrate was very different between the 2021 and 2022 seasons (**Figure 2**). I expected to find most nests in small deciduous shrubs which was the case in 2021, but this was not the case in 2022. In 2021, 78% of nests were found in expected vegetation types like *Diospyros texana* (n = 7), *Lonicera albiflora* (n = 3), *Dermatophyllum secundiflorum* (n = 2), *Rhus virens* (n = 1), or *Berberis trifoliolata* (n = 1) while 22% were found in *Juniperus ashei* (n = 3) and *Pinus remota* (n = 1). However, in 2022, only 56% of nests were found in expected vegetation types: *D. texana* (n = 2), *D. secundiflorum* (n = 3), *R. virens* (n = 3), and *Quercus fusiformis* (n = 1), whereas 44% of nests were found in *J. ashei* (n = 7) in 2022. For the purpose of analysis, nest substrates

were categorized as either non-coniferous (expected nest substrate) or coniferous (not expected).

All combinations of models containing year, nest height, nest substrate, and Julian date of discovery (and their interactions) were considered (**Table 1**). The most influential model was the model that contained year, nest substrate, and the interaction between height and Julian date of discovery (ΔAIC = 0, wt = 0.995; **Table 2**). When considering the year a nest was found, 2021 was the reference category and 2022 negatively influenced daily survival rate (β = -0.0759; SE = 0.00143; p < 0.01). On a nest site scale, nests in non-coniferous substrate, with coniferous substrate as the reference category, and height of the nest were both positive influences on daily survival rate ($\beta_{substrate}$ = 0.0119; $SE_{substrate}$ = 0.00155; $p_{substrate}$ < 0.01; β_{height} = 0.0369; SE_{height} = 0.0447; p_{height} = 0.416). Julian discovery date also positively influenced daily survival rate (β = 0.000205; SE =0.000207; p = 0.331). Nest height did not seem to influence daily survival rate (**Figure 3**). There was a similar relationship between daily survival rate and Julian date for nests in 2021 as those values stayed fairly constant (**Figure 4**). There were a few instances in 2022 where nests found earlier were less successful and nests found later were more successful when compared to the majority of nests found in that year (**Figure 4**). Using the logistic exposure method for calculating nest success, a theta value was determined. The theta value represents the likelihood that a nest will survive the interval between nest checks. Nests found in 2021 had fairly constant theta values while nests found in 2022 had theta values with more variation between them (**Figure 5**). Overall daily survival rates were once again higher in 2021 than in 2022 and it was found that the range of

values in 2021 was smaller than the range of values in 2022, illustrating how drought conditions can influence nest success (**Figure 6**).

Nesting success was lower in 2022 than it was in 2021. The average daily survival rate was 0.96 and 0.88 in 2021 and 2022, respectively. The annual survival for 2021 was 40.5% and only 4.6% for 2022, a drastic decrease (**Figure 7**).

Discussion

Black-capped Vireos had higher reproductive success when they built nests in a non-coniferous nest substrate, the expected type of nest substrate for the species. Additionally, nests found in 2022 were less successful than those found in 2021. Both of these are important variables to take note of because there was an increase of coniferous substrate use in 2022 that may explain the discrepancy between survival rates. My data showed that the daily survival rate was fairly constant throughout the breeding season of 2021, but in 2022, early nests were less successful and late nests were more successful when compared to the majority of daily survival rates. This contrasts from previous research that found that daily survival rate decreases later into the breeding season (Kovar et al. 2018). It is possible that small sample size in our dataset may have resulted in a bias toward daily survival rate. It is also probable that there are underlying regional factors of each that explain this discrepancy, because much of the previous research on Black-capped Vireos has taken place in central Texas rather than the southwestern region.

Common nest predators (e.g., snakes and birds) are both known to use visual cues to lead them to active nests and increased parental activity around the nest can tend to lead to depredation events (Mullin and Cooper 1998, Robinson and Robinson 2001). This

has been seen in Black-capped Vireos because as eggs hatch and nestlings need to be cared for. Adults must leave and return to the nest with increased frequency and that nest stage plays a major role in influencing daily survival rates (Conkling et al. 2012). With nest substrate being drier, and therefore providing less cover, in 2022 we saw higher depredation events leading to lower daily survival rates overall. These results may have been caused by nest building activities and incubation change-over events facilitating location of nests by predators. Mammalian species are also known to be predators of nesting Black-capped Vireos however, studies found that this group accounted for a small amount of depredation events at Fort Hood (Tazik 1991). However, Conkling et al. (2012) found that depredation by snakes was lower in southwest Texas due to the hot, arid environment forcing individuals to forage during cooler nocturnal periods.

The drought conditions of the 2022 field season demonstrated that in any given year, there are events that can lead to reduced productivity for Black-capped Vireos. In the case of this breeding season, reduced productivity took the form of a decreased daily survival rate that will result in fewer young being added to the population. There are other measures of productivity such as young produced per successful nest or fecundity that were not addressed in this study. This is important to note because as the climate continues to change and these drastic events become more frequent, population models will need to factor in the possibility of reduced productivity when considering what healthy population sizes are sustainable. Black-capped Vireos were shown to start their molt process significantly earlier in a drought year than a wet year (Butler et al. 2008). Additionally, because Black-capped Vireos are likely to re-nest after a failure (Grzybowski et al. 1994), the length of the breeding season can be extended which can

cause later molt patterns resulting in faster feather production that leads to lower quality feathers (Dawson et al. 2000, Dawson 2004). All of this can then be related to a reduced winter survival followed by reduced reproductive success on a population scale from less surviving individuals, meaning that nest predation and nest parasites can affect a species success both directly and indirectly (Nilsson and Svensson 1996, Butler et al. 2008).

As noted earlier, the drought conditions have shown Black-Capped Vireos to nest in Ashe juniper more than normal. Increased environmental stress can take many forms, including harsh breeding season weather or changes in habitat structure, and how one species responds will be unique from others in the same area (Holmes et al. 1986). Continued monitoring of the species is warranted as part of post delisting monitoring to determine long-term population trends. Additionally, since the species requires successional scrubland habitat to breed, areas that were once suitable for breeding may become unsuitable over time (Gryzbowski 2020). While occupying a small breeding range, it is noted that the eastern limits of this range contain more mesic habitat and western limits contain more xeric habitat that will lead to differences in management styles across the breeding range (Gryzbowski 2020). Research conducted at Fort Hood, Texas, investigated nest success in two different habitat types within the installation. They found that nests built in the lower quality human-made habitat experienced lower nest success than those built in shrubland habitat (Noa et al. 2007). Lower nest success in 2022 could be due to lower quality nesting substrate however, it is unclear whether Ashe juniper by itself is a low quality nest substrate or drought conditions result in lower vegetation quality across all species regardless of type.

Our results show that in the western portions of their breeding range, Ashe juniper has become an important secondary source of nest substrate for Black-capped Vireos. In Oklahoma, Gryzbowski et al. (1986) noted that the vireos can tolerate junipers if they do not disrupt the growth and distribution of their preferred habitat but will underutilize it (Gryzbowski et al.1986). Another study from Fort Hood found that Black-capped Vireos were 283% more likely to nest in deciduous substrates than juniper and that, in habitats with lessened disturbances, juniper could outcompete deciduous plants (Fonteyn et al. 1988, Bailey and Thompson 2007). In spite of this, it appears that Ashe juniper is necessary for Black-capped Vireos when vegetation cover cannot be obtained from other species of nest substrate. This is because Ashe juniper is a drought-tolerant species that is adapted in obtaining water from sources farther beneath the surface than the deciduous species that Vireos normally use for nest substrate (Gilman and Watson 1993, Jackson et al. 1999). Additionally, it was found that in the 2011 historic drought in Texas, Ashe juniper was consistently green and likely provided ample cover for Black-capped Vireos (Colon et al. 2017). Disturbance events, like fire, can kill or slow juniper growth which in turn helps promote the growth of early successional deciduous shrubs (Fonteyn et al. 1988). As it turns out, the southwest portion of the breeding range is more prone to natural disturbance events that may destroy habitat and slow the successional changes of the area due to lower rainfall (Smith-Hicks et al. 2017).

The Texas A&M Forest Service collects live fuel moisture content data throughout the state with one location being Kickapoo Cavern State Park, collecting samples of Ashe juniper, live oak, and honey mesquite. Fuel moisture content tells us the percentage of a fuel's weight in water compared to its dry weight in order to show how

dry certain areas are for risk of fire. These tests show that all species had percentages that were lower than both their 2021 values and their average values indicating that conditions were drier in 2022. Noa et al. (2007) found in their two-year study that in 2003, the breeding season was much drier than 2004 and this resulted in much lower daily survival rates in 2003.

Both Ashe juniper and live oak can be used as nest substrate for Black-capped Vireos and since Ashe juniper was less dry in the month of May, the beginning of breeding season, it seems intuitive that the species started to build nests in an unexpected substrate, given the environmental conditions. Other previous research by Smith-Hicks et al. (2017) supports our findings that in the southwestern portions of their range the vireos will utilize Ashe juniper as nesting substrate more than eastern counterparts, indicating that management practices need to weigh habitat constraints of the breeding range as a whole. Their research was collected in 2009 and 2010, before the historic drought, which adds a new wrinkle into juniper use by the vireos and perhaps indicates that the southwestern portions of the breeding range exhibit harsher conditions, on a more frequent basis, than those in the east.

Management Implications

The drought conditions of the 2022 field season indicate that in any given breeding season, environmental conditions can result in extremely low nest survival for Black-capped Vireos. This is important to note because as the climate continues to change and these drastic events become more frequent, population models will need to factor in the lack of productivity when considering what healthy population sizes are sustainable. As noted earlier, the drought conditions have shown Black-capped Vireos to

nest in Ashe juniper more than normal. A common management practice of the

southwestern Edwards Plateau is to remove juniper, both for creation of Vireo habitat as

well as for other land management purposes. Results of this study may help inform land

managers that Ashe juniper is beneficial to keep around as a necessary nest substrate as

exceptional drought conditions become more common.

II. THE INFLUENCE OF VARIED-SCALE CHARACTERISTICS ON BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*) PARASITISM OF BLACK-CAPPED VIREO (*VIREO ATRICAPILLA*) NESTS IN THE SOUTHWESTERN EDWARDS PLATEAU

Introduction

Black-capped Vireos (*Vireo atricapilla*) were included on the U.S. Endangered Species List from 1987 to 2018 due to nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) and loss of breeding habitat to development and natural vegetative succession. Continued monitoring of the species is warranted as part of post delisting monitoring to determine long-term population trends. Additionally, since the species requires successional scrubland habitat to breed, areas that were once suitable for breeding may become unsuitable overtime (Gryzbowski 2020). While occupying a small breeding range, it is noted that the eastern limits of this range contain more mesic habitat and western limits contain more xeric habitat that will lead to differences in management styles across the breeding range (Gryzbowski 2020). The sites in our study fall in the western portion of this range.

Additionally, parasitism by Brown-headed Cowbirds is a threat that negatively impacts population numbers and should be monitored. Brown-headed Cowbird parasitism is more prevalent in the eastern portion of the Black-capped Vireo's breeding range but landscape factors and population sizes, among other things, may influence sustainable parasitism rates (USFWS 2018). It is important to note that the USFWS recommends a parasitism rate of less than 40% for management purposes (USFWS 2016).

This study will attempt to assess the factors of nest site selection that lead to reducing brood parasitism to better inform management decisions made around the Black-capped Vireo's breeding habitat.

Methods

<u>Species Description</u>

The Black-capped Vireo (*Vireo atricapilla*) is a foliage gleaning songbird belonging to the family Vireonidae that breeds from Oklahoma through central and southwestern Texas and into northern Mexico. Black-capped Vireos are unique among vireos by being sexually dichromatic to humans viewing them in the field (Grzybowski 2020). Males have a dark black cap that forms spectacles around the eyes while females and immature males have a similar cap that is a duller gray than mature males. Major threats to their population include Brown-headed Cowbird brood parasitism and loss of breeding habitat through destruction or natural successional changes (Grzybowski 2020). After being placed on the Endangered Species List in 1987, the species has been recovering and recent surveys between 2009 and 2014 have shown the population had grown to 5,244 adult males (United States Fish and Wildlife Service [USFWS] 2018). With the recent growth in population, the species was removed from the U.S. Endangered Species List but remains of conservation concern and is listed as near threatened by the IUCN Red List (2021).

The species prefers to nest in areas with low-growing, shrubby mottes of vegetation with spaces and openings within the vegetation that is generally either early successional or in edaphic settings like gullies, ravines, and slopes (Graber 1961, Grzybowski 2020). In the Edwards Plateau the vireos are found in areas of deciduous scrubland with vegetation ranging in height from 0–2 meters (Grzybowski et al. 1994). While its range is rather small, there is a large variety of plant species that provide ideal habitat for the Black-capped Vireo. Some of the plant species most frequently encountered across the breeding range are species of oaks (*Quercus* spp.), sumacs (*Rhus* spp.), Texas persimmon (*Diospyros texana*), roughleaf dogwood (*Cornus drummondii*),

and redbud (*Cercis canadensis*) (Graber 1957, Tazik et al. 1993, Benson and Benson 1990, Grzybowski et al. 1994, Grzybowski 2020). In Texas, this type of vegetation is commonly found in areas with Fredericksburg limestone that supports poor soils (Grzybowski 2020). Other areas of the breeding range, Oklahoma and Mexico, contain different species of vegetation that the vireos have been found to nest in including blackjack oak (*Q. marilandica*), post oak (*Q. stellata*), madrone (*Arbutus xalapensis*), lantrisco (*Rhus pachyrrachis*), orchid tree *(Bauhinia ramossisima)*, and thickleaf milkberry (*Chiococca pachyphylla*) (Graber 1961, Gonzalez-Rojas et al. 2014).

<u>Study Site</u>

Kickapoo Cavern State Park is a 2,577 hectare (6,368 acre) state park owned and operated by Texas Parks and Wildlife Department (TPWD) that lies north of Brackettville, Texas, straddling the Kinney/Edwards County line. Before being acquired by TPWD in 1986, the land was owned by the Seargeant Ranch. The park is characterized by a mosaic of vegetation from three different natural regions of Texas including live oak-juniper woodlands of the Edwards Plateau, thorny shrubs of the South Texas Brush Country, and cacti of the Trans Pecos (Texas Parks and Wildlife Department 2020). The wide variety of vegetation allows for a large number of bird species to inhabit the park as both migrants and residents, including the Golden-cheeked Warbler and Black-capped Vireo. Kickapoo Cavern State Park is listed as "Manageable" with 64 males at the last official census of Black-capped Vireos for the park, per the Post Delisting Monitoring Plan (USFWS 2018).

<u>Survey Protocol</u>

I assessed nest success and parasitism rates by using a nest searching and monitoring protocol. Nest searching and monitoring occurred from the beginning of May until the middle of July of 2021 and 2022. Nests were found by following standard nest searching and monitoring protocols outlined by Martin and Geupel (1993) and monitoring for nesting behavior such as singing males, courting behavior, and birds with food or nesting material in their mouths. Locations that were found to have any of the listed activities, but did not result in finding a nest, were recorded and searched at a later date because these behaviors indicated a nest was likely present and extended human activity could cause nest abandonment or depredation.

At each nest, I recorded nest substrate, nest height, orientation of nest, and the date it was located. GPS coordinates for the nest were recorded both manually (e.g., data sheet) as well as on electronic devices (e.g., Garmin GPS and the ArcGIS Collector app). Flagging tape was placed on a nearby tree to further facilitate re-locating nests. A compass direction was taken from the flag facing towards the nest, with a distance estimation from the flag to the nest, both recorded on the data sheet.

Once located, nests were monitored every 3–5 days as conditions permitted (USFWS 2018). Nest checks were conducted by nest pole camera (e.g., smartphone attached to selfie stick) so nest contents could be observed away from the nest. This method helped minimize disturbance to the nest, as well as prevented leaving a scent to attract mammalian predators or drawing the attention of avian predators from parental alarm calls. At each nest check, including the first time a nest is found, I recorded the date of the check, number of eggs in the nest (both BCVI and BHCO if present), and number of nestlings (both BCVI and BHCO if present and at that stage). Notes were

taken at each check for anything significant that happened. Examples of significant events at the nest included evidence of nest building, flushing a bird off the nest, or evidence of predation upon discovering a failed nest.

Finally, I determined nest fate (i.e., success or failure) based on evidence at and around the nest. Nest success was defined as evidence of fledglings (begging, parents feeding, etc.) present at or near the nest. Nest failure was determined based on nest contents and potential signs in and around the nest. I assumed that if a nest was empty upon that check and the nest was either still at the incubation stage or too early for fledging, then the nest had been depredated. I assumed that a nest had been abandoned causing failure if there was no parental activity around the nest for consecutive checks, equaling about a week in time.

Statistical Analyses

All statistical analyses were completed using the statistical program R version 4.2.1 (R Core Team, Vienna, Austria). I created *a priori* models to evaluate the influence of different covariates and their interactions on the presence or absence of brood parasitism. Some covariates were on a temporal scale (Year, Julian date of discovery), while others were at the nest-site scale (Nest substrate, Nest height). Presence of brood parasitism was used as the response variable to assess the fit of the models using an information theoretic approach (Burnham and Anderson 2002). Models were selected using Akaike Information Criterion (AIC) where the lowest AIC was the selected model when there were no competing models. Competing models were those with $\Delta AIC \leq 2$ and in this case, the most parsimonious model was selected.

Nest Parasitism – Overall nest parasitism rate was calculated for each year of the study. This was achieved by taking the total number of Black-capped Vireo nests that had at least one Brown-headed Cowbird egg or nestling present and dividing it by the total number of nests found in that year.

Results

In 2021, a total of 22 nests were found and monitored; four of these nests were found after fledglings left the nest and were excluded from analysis. A total of 33% of these nests (n = 6) were parasitized by Brown-headed Cowbirds. The 2022 season resulted in only a total of 15 nests being found and monitored; 47% of these nests (n = 7) were parasitized by Brown-headed Cowbirds during the season, with two of them resulting in a cowbird fledging from the nest.

Nest substrate was very different between the 2021 and 2022 seasons (**Figure 2**). We expected to find most nests in small deciduous shrubs which was the case in 2021, but 2022 showed us the opposite. In 2021, 78% of nests were found in expected vegetation types like *Diospyros texana* (n = 7)*, Lonicera albiflora* (n = 3)*, Dermatophyllum secundiflorum* (n = 2)*, Rhus virens* (n = 1), and *Berberis trifoliolata* (n = 1) while 22% were found in *Juniperus ashei* (n = 3) and *Pinus remota* (n = 1). However, in 2022, only 56% of nests were found in expected vegetation types: *D. texana* (n = 2), *D. secundiflorum* (n = 3), *R. virens* (n = 3), and *Quercus fusiformis* (n = 1). 44% of nests were found in *J. ashei* (n = 7) in 2022. For the purpose of analysis nest substrates were categorized as either non-coniferous (expected nest substrate) or coniferous (not expected).

All combinations of models containing year, nest height, nest substrate, and Julian date of discovery (and their interactions) were considered (**Table 3**). There were two competing models, the model that contained only nest substrate (ΔAIC = 0, wt = 0.414; **Table 4**) and the model that contained year, nest height, and nest substrate (ΔAIC = 1.94, wt = 0.157; **Table 4**). The nest substrate only model was selected for parsimony. When considering the nest substrate, with coniferous substrate as the reference category, nests in non-coniferous substrate positively influenced the presence of Brown-headed Cowbird parasitism ($\beta_{substrate}$ = 2.485; $SE_{substrate}$ = 1.133; $p_{substrate}$ = 0.0282).

Of the nests that were not parasitized, 50% were in non-coniferous substrate (n = 10) and 50% were in coniferous substrate (n = 10). Nests that were parasitized were not as evenly split. 92% (n = 12) of the parasitized nests were found in non-coniferous substrate while only 8% (n = 1) of parasitized nests were found in coniferous substrate. The percentage of parasitized nests increased in 2022 when compared to the 2021 numbers, even with fewer total nests found (**Figure 8**). The majority of parasitized nests were those placed below one meter in height (n = 10) and I did not see a trend indicating that parasitism is increased in nests that are placed higher in the substrate (**Figure 9**).

Discussion

Parasitism by Brown-headed Cowbirds is a threat that negatively impacts population numbers and should be monitored. Brown-headed Cowbird parasitism is more prevalent in the eastern portion of the Black-capped Vireo's breeding range, but landscape factors and population sizes, among other things, may influence sustainable parasitism rates (USFWS 2018). It is important to note that the USFWS recommends a parasitism rate of less than 40% for management purposes (USFWS 2016). Previous

research found a higher parasitism rate in the drought year of 2011 than in 2012 and captured female cowbirds in 2012 had reduced body condition that resulted in reduced breeding efforts as a result of surviving through the drought (Buxton et al. 2018). This seems to indicate that next year's vireos may experience less parasitism as a result of the 2022 drought. Two studies from Fort Hood, Texas, and surrounding areas found that the lower parasitism rates in 2012 resulted in significantly higher nest success than in 2011 (Walker et al. 2016, Buxton et al. 2018). A study that took place close to my study site found much higher nest success in the non-drought year compared to the drought year and that parasitism rates were significantly lower in those years as well (Colon et al. 2017). This pattern is similar to the pattern seen in my data. Black-capped Vireos seem to be more vulnerable to brood parasitism when compared to White-eyed Vireos (*Vireo griseus*) and Northern Cardinals (*Cardinalis cardinalis*), two co-occurring species, and cowbird trapping resulted in higher daily survival rate (Campomizi et al. 2013).

Identifying source and sink populations can be crucial to conservation of threatened and endangered species. Source populations are those with high reproductive output and therefore require young to disperse away from their natal grounds while sink populations are those that lack a sufficient reproductive output and rely on immigrants from source populations to avoid local extinction (Brown and Kodric-Brown 1977, Pulliam 1988). Using population growth models, researchers predicted the viability of three songbird populations in fragmented and contiguous habitats where results showed that fragments acted as population sinks and contiguous forest acted as population sources (Donovan et al. 1995). Warbling Vireos (*Vireo gilvus*) in British Columbia face a large threat due to brood parasitism. This research showed that Warbling Vireos at

lower elevations were subject to higher levels of brood parasitism than those that nest at higher elevations due to timber harvesting and that the low elevation populations need to rely on immigrants from high elevations to avoid local extinction (Ward and Smith 2000). Specifically in Black-capped Vireos, locations that employed some method of cowbird control had higher success than those without, although they were not static and had some level of temporal variation (Walker et al. 2016). It will be important to monitor parasitism rates to see if vireo populations become more productive following a drought event and perhaps offset the reduced reproductive output of drought years.

It is also possible that nesting in Ashe juniper represents an "ecological trap" for Black-capped Vireos. An ecological trap occurs when an animal makes a poor habitat choice based on former habitat cues that no longer represent high quality habitat due to sudden changes in that environment (Schlaepfer et al. 2002). Research conducted on Indigo Buntings () found that they preferred to nest in experimentally manipulated patches that created more edge habitat, but this resulted in higher nest predation rates for those nests (Weldon and Haddad 2005). In 2022, juniper appeared to provide a better quality nest substrate however, the nesting success was far lower than it was in 2021 so using Ashe juniper turned out to be non-beneficial for the species. Weldon and Haddad (2005) determined that ecological traps may have more of an effect on birds that are not capable of double broods, as they cannot make up for the lower early-season nest success. However, their study site was in a forested landscape where brood parasitism was not high and they determined that areas with higher parasitism threats could be at a greater risk for severe effects of these traps (Weldon and Haddad 2005). This is important to consider because while Black-capped Vireos are known to be threatened by Brown-

headed Cowbird parasitism, they are also capable of renesting during the breeding season (Pease and Grzybowski 1995).

It is interesting to note that even with more nests being found in coniferous trees in 2022, there was still a large difference in which substrate had more parasitism. It is logical to assume that there would be a higher number of nests in the dominant substrate that result in nest parasitism simply because that is where the most nests are being found. Interestingly, there were far more coniferous trees being used as nest substrate in 2022 yet there was only one case of nest parasitism in these nests between both years. Perhaps this speaks to a coniferous substrate providing more protection from a prospective nest parasite. In previous studies on various species of songbirds, results have shown that parasitism can fluctuate between years depending on numerous factors including management practices (Morrison and Averill-Murray 2002, Kostecke et al. 2005, Campomizzi et al. 2013).

Sharp and Kus (2006) found that for Least Bell's Vireos, unparasitized nests were those that had high microhabitat cover (Sharp and Kus 2006). This could help explain why Black-capped Vireo nests located in coniferous substrate experienced less brood parasitism, even when that became the dominant nest substrate. The coniferous nest substrates of this region are evergreen and provide thicker leaves that will provide more cover in a drought year when deciduous trees cannot produce enough leaves. Similarly, conifers can potentially provide more cover even in non-drought years when compared to non-coniferous substrates.

Previous research found that vireos that nested earlier were at a lower risk of being parasitized and there was no evidence that nesting earlier led to higher predation

rates, including by snakes (Sperry et al. 2008, Boves et al. 2014). Perhaps arriving earlier to the breeding grounds could provide an alternative to combat higher levels of parasitism. Vireos in the study region will frequently use Texas mountain laurel, an evergreen plant, as a nest substrate but since this is not their only source of nest substrate and others are deciduous, there may be a trade-off with early arrival to the breeding grounds to nest before leaf-out occurs. However, as the climate continues to change, there is an effect of spring leaf-out on deciduous plants that has been driven earlier with warmer spring temperatures (Fu et al. 2019). Data from the USA National Phenology Network shows that spring leaf-out is predicted to come 10 days earlier than the long-term average (USA National Phenology Network 2023). Also, brood parasitism frequency was not associated with woody cover or edge density of Black-capped Vireo nests (Campomizi et al. 2013). Female Brown-headed Cowbirds appear to use surrounding trees as perches to search for potential host nests (Clotfelter 1998). This is why many studies have found a link between increased parasitism with nests placed higher in the nest substrate, however, my data did not reflect this pattern.

Management Implications

Monitoring the rates of Brown-headed Cowbird parasitism is an important component of Black-capped Vireo conservation. In years where apparent reproductive success is extremely low (as in 2022), it is even more important to take note of parasitism rates. Some amount of parasitism is expected and can be overcome to allow a population to continue to grow. Black-capped Vireos may benefit from added Brown-headed Cowbird management during years of exceptional drought to combat all the other factors they face to have a successful nest. Adaptive management programs during these years

could include increased trapping and removal of cowbirds or removal of cowbird eggs from nests that are being actively monitored. Additionally, it appears that non-coniferous nest substrates provide some sort of buffer against nest parasitism. From a management perspective, this is another reason that removal of Ashe juniper may do more harm than good for Black-capped Vireos.

TABLES

Table 1. All nest success models tested using AIC.

Model No.	Model
1	$B0 + B1$ X Year $+ B2$ X Height $+ B3$ X Substrate $+ B4$ X ObsDate
2	$B0 + B1$ X Year $+ B2$ X Height $+ B3$ X Substrate
3	$B0 + B1$ X Year $+ B2$ X Height
4	$B0 + B1$ X Year
5	$B0 + B1$ X Height $+ B2$ X Substrate $+ B3$ X ObsDate
6	$B0 + B1$ X Height $+ B2$ X Substrate
7	$B0 + B1$ X Height
8	$B0 + B1$ X Substrate $+ B2$ X ObsDate
9	$B0 + B1$ X Substrate
10	$B0 + B1$ X ObsDate
11	$B0 + B1$ X Year $+ B2$ (Height X Substrate) $+ B3$ X ObsDate
12	$B0 + B1$ X Year $+ B2$ (Height X ObsDate) $+ B3$ X Substrate
13	$B0 + B1$ X Year $+ B2$ X Height $+ B3$ (Substrate X ObsDate)
14	$B0 + B1$ (Year X Sub) $+ B2$ X Height $+ B3$ X ObsDate
15	$B0 + B1$ (Year X Height) $+ B2$ X Substrate $+ B3$ X ObsDate

Table 2. Selected model for daily survival rate based on AIC.

Model No.	Model	Rank	K	LL	AICc	Delta	Weight
12	$B_0 + B_1 \times Year + B_2 (Height \times ObsDate) + B_3 \times Substrate$	1	4	394.810	-774.9	0	0.995

Table 3. All parasitism models tested using AIC.

Model No.	Model
1	B0 + B1 X Year + B2 X Height + B3 X Substrate + B4 X ObsDate
2	B0 + B1 X Year + B2 X Height + B3 X Substrate
3	B0 + B1 X Year + B2 X Height
4	B0 + B1 X Year
5	B0 + B1 X Height + B2 X Substrate + B3 X ObsDate
6	B0 + B1 X Height + B2 X Substrate
7	B0 + B1 X Height
8	B0 + B1 X Substrate + B2 X ObsDate
9	B0 + B1 X Substrate
10	B0 + B1 X ObsDate
11	B0 + B1 X Year + B2 (Height X Substrate) + B3 X ObsDate
12	B0 + B1 X Year + B2 (Height X ObsDate) + B3 X Substrate
13	B0 + B1 X Year + B2 X Height + B3 (Substrate X ObsDate)
14	B0 + B1 (Year X Sub) + B2 X Height + B3 X ObsDate
15	B0 + B1 (Year X Height) + B2 X Substrate + B3 X ObsDate

Table 4. Selected model for parasitism based on AIC

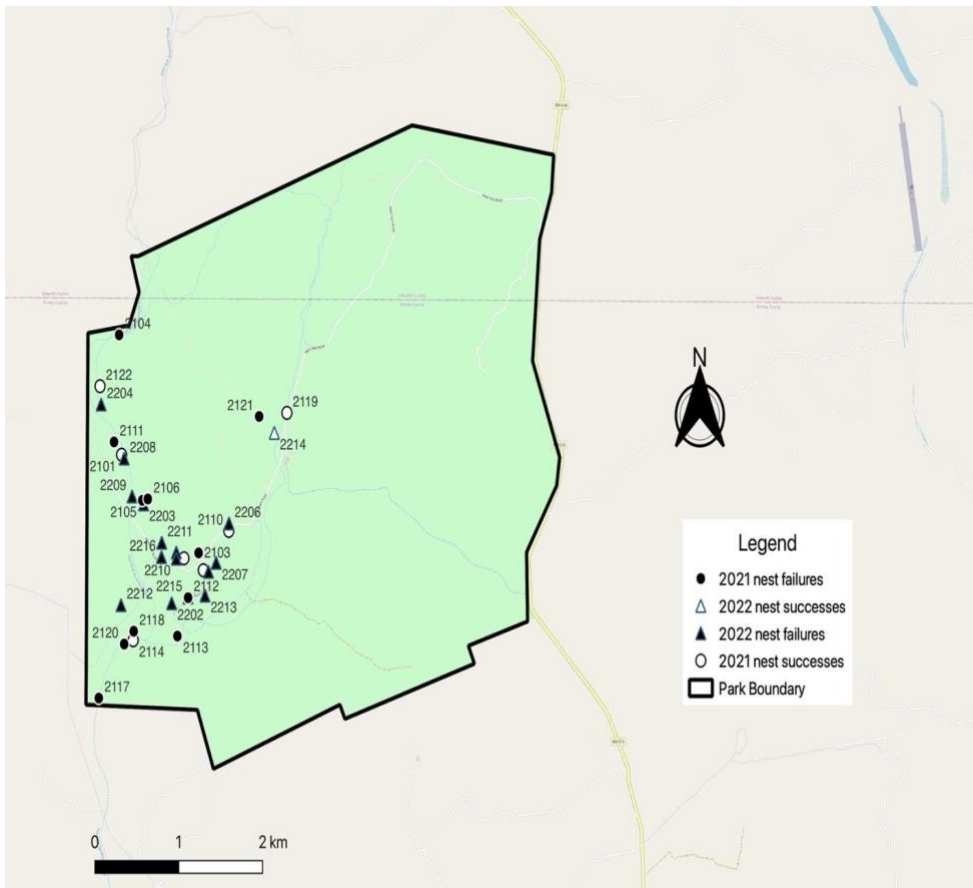| Model No.	Model	Rank	K	LL	AICc	Delta	Weight
10	$B_0 + B_1$ X Substrate	1	2	-18.509	41.4	0	0.414

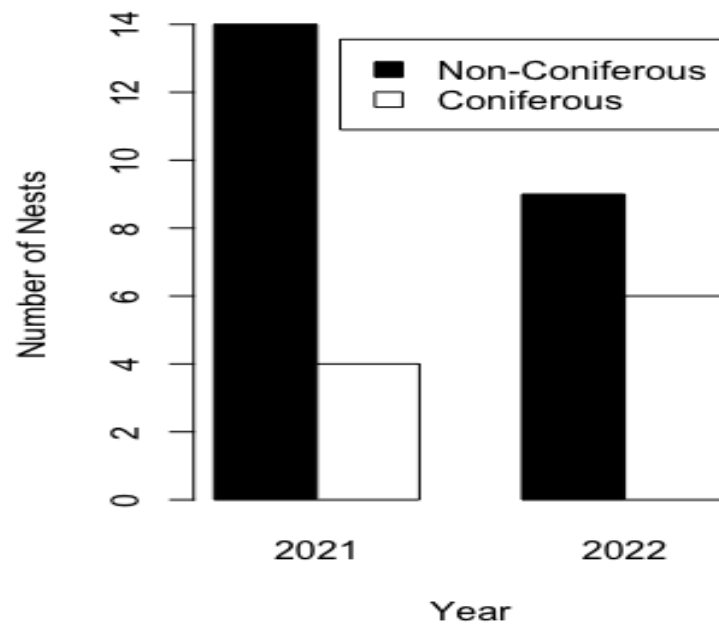Figure 1. Locations of all Black-capped Vireo nests monitored.

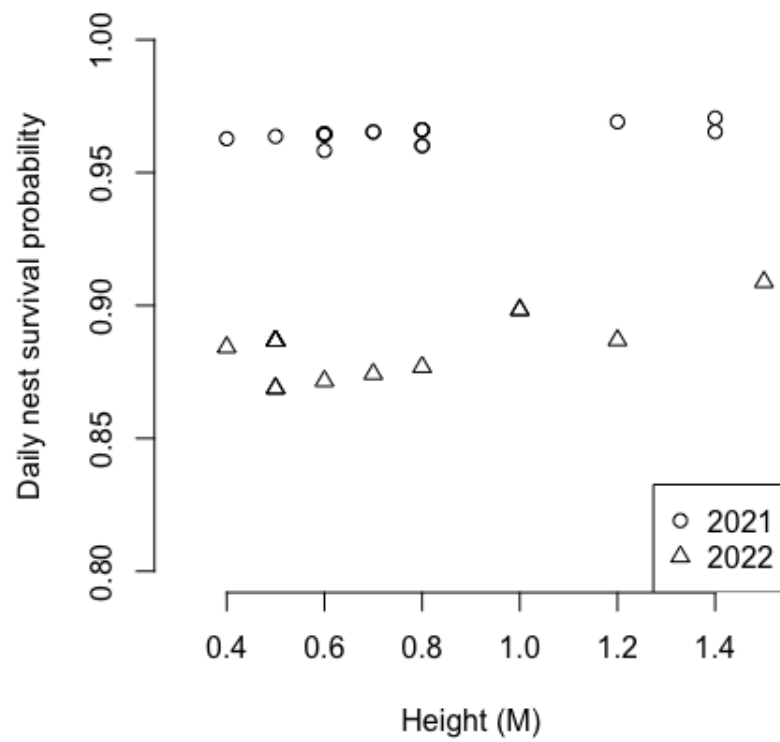Figure 2. Distribution of Black-capped Vireo nests by nesting substrate between years.

Figure 3. Daily survival probability of Black-capped Vireo nests based on nest placement height.
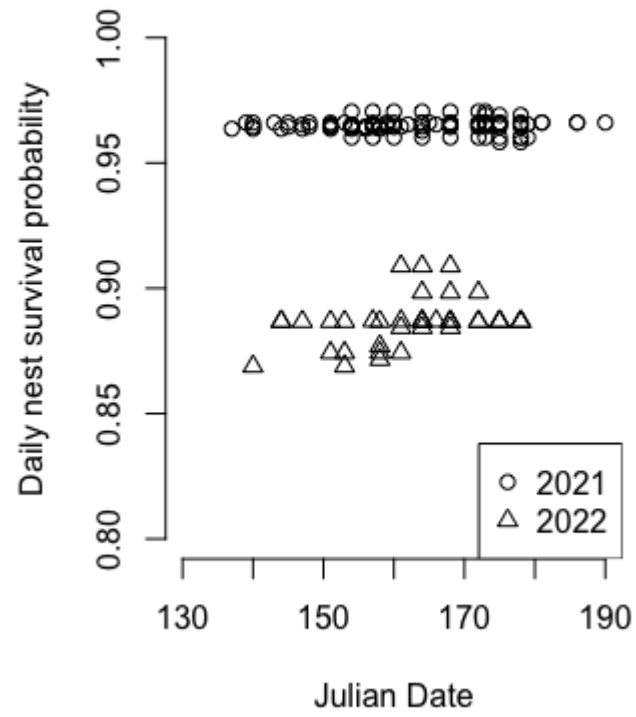
Figure 4. Daily survival probability of Black-capped Vireo nests based on Julian date.
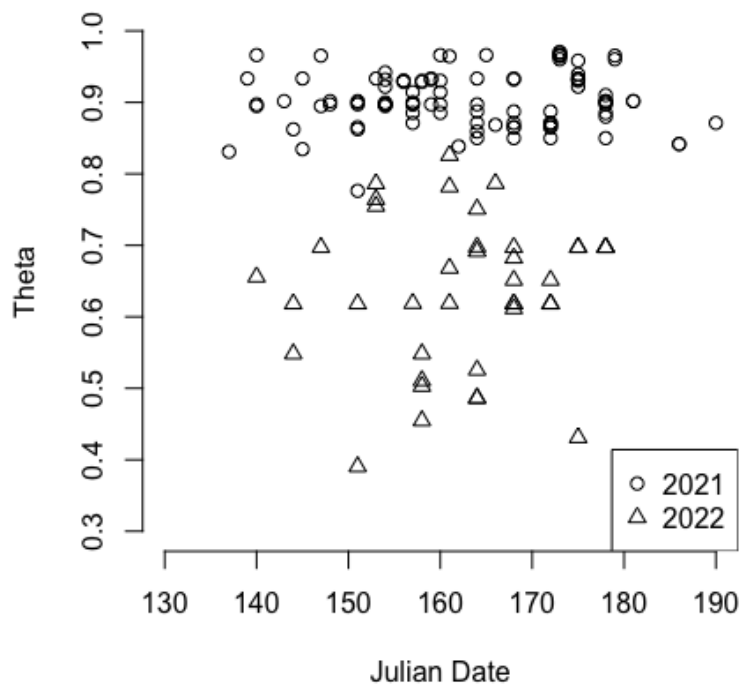
Figure 5. Predicted theta value of Black-capped Vireo nests in 2021 and 2022 based on the Julian date the nest was discovered. Theta values are the probability a nest survives a nest check interval.
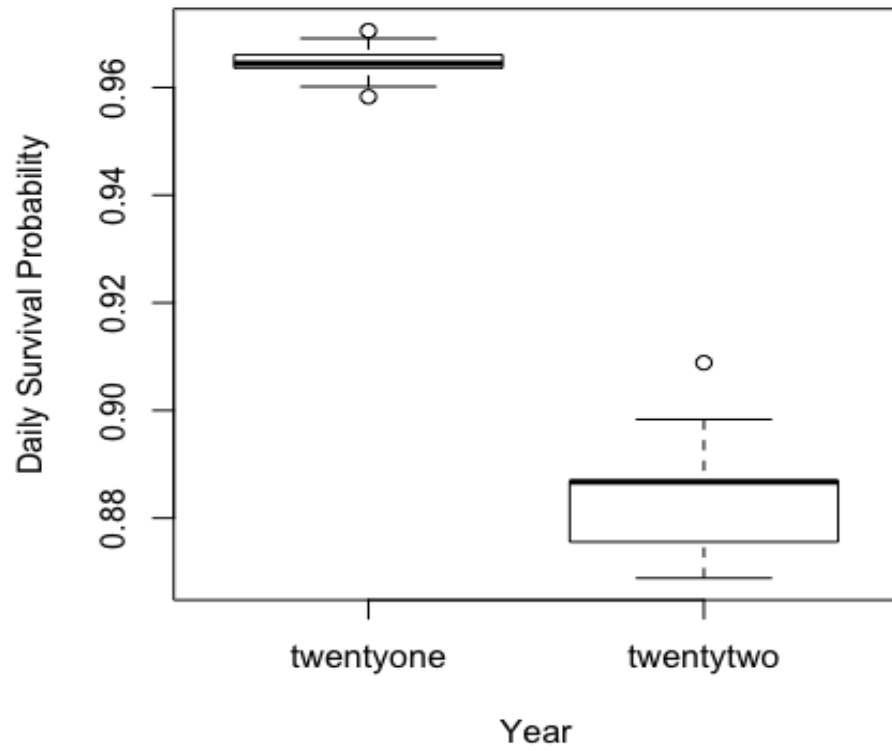
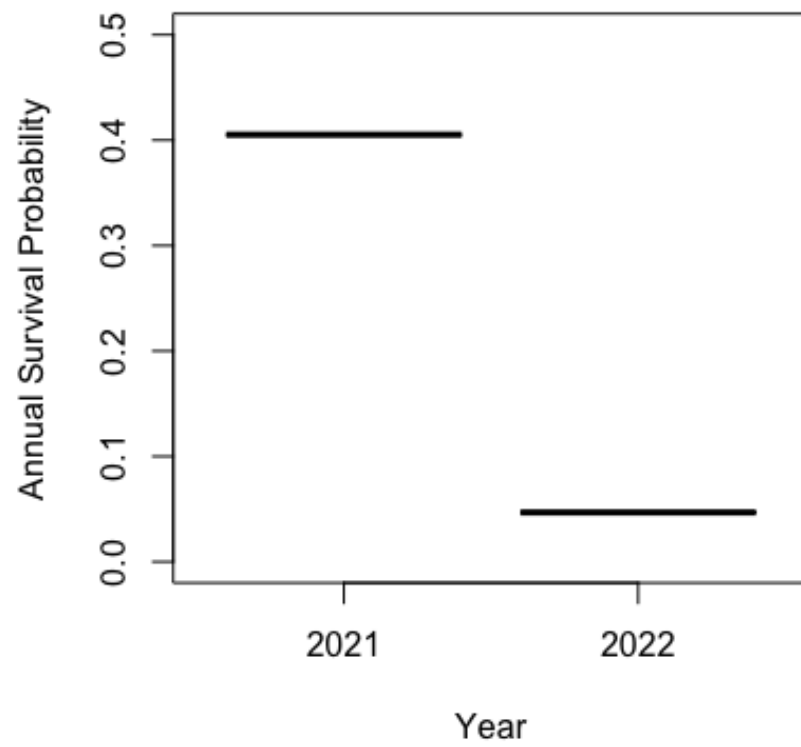Figure 6. Average daily survival rate for Black-capped Vireo nests in 2021 and 2022.

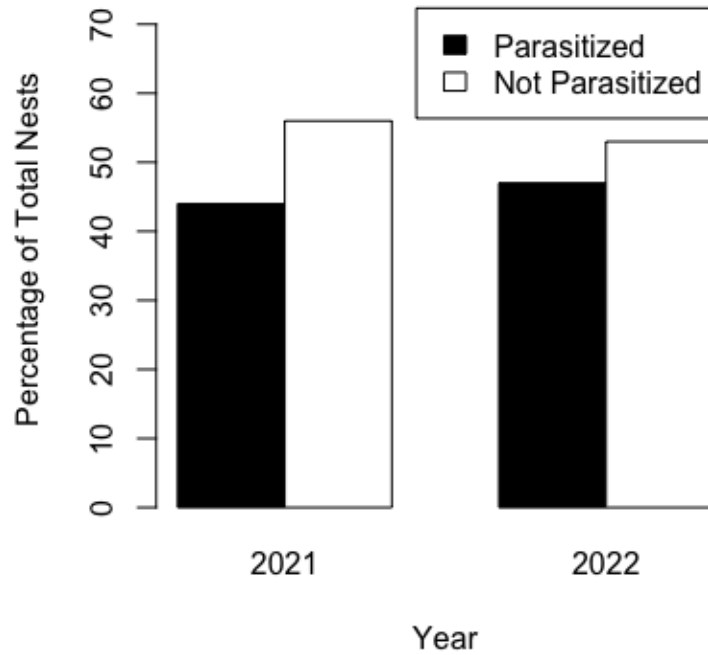Figure 7. Predicted annual survival rate of Black-capped Vireo nests in 2021 and 2022.

Figure 8. Percentage of Black-capped Vireo nests that were parasitized by Brown-headed Cowbirds in 2021 and 2022.
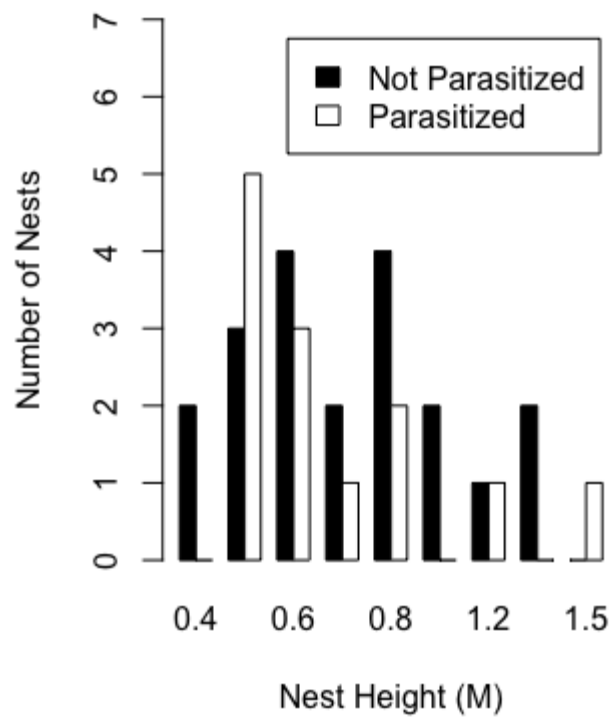
Figure 9. Total number of Black-capped Vireo nests parasitized by Brown-headed Cowbird compared to those not, by height of nest in meters.

LITERATURE CITED

Bailey, J. W., and F. R. Thompson III. 2007. Multiscale nest-site selection by Black-capped Vireos. Journal of Wildlife Management 71(3): 828–836.

Benson, R. H. and K. L. P. Benson. 1990. Estimated size of Black-capped Vireo populations in Coahuila, Mexico. Condor 92:777–779

Bent, A. C. 1965. *Life histories of North American wagtails, shrikes, vireos, and their allies*. Washington D.C., USA: Smithsonian Institution.

Boves, T. J., J. H. Sperry, K. Comolli, and P. J. Weatherhead. 2014. Brood parasitism of Black-capped Vireos: frontline and post-laying behavioral responses and effects on productivity. Journal of Field Ornithology 85(4): 364–378.

Brown, J. H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on long-term census data. Ecology 77: 3–12.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Butler, L. K., T. J. Hayden, and L. M. Romero. 2008. Prebasic molt of Black-capped and White-eyed Vireos: effects of breeding site and the El Niño-Southern Oscillation. Condor 110(3): 428–440.

Buxton, V. L., W. M. Schelsky, T. J. Boves, S. Summers, P. J. Weatherhead, and J. H. Sperry. 2018. Effects of drought on brood parasite body condition, follicle development, and parasitism: Implications for host-parasite dynamics. Auk 135(4): 908–918.

Campomizi, A. J., H. A. Mathewson, M. L. Morrison, C. M. Lituma, T. J. Conkling, M. C. Cocimano, S. L. Farrell, R. N. Wilkins, and J. A. Butcher. 2013. Understanding nest success and brood parasitism in the endangered Black-capped Vireo: comparisons with two sympatric songbirds. Wilson Journal of Ornithology 125(4): 709–719.

Clotfelter, E. D. 1998. What cues do Brown-headed Cowbirds use to locate Red-winged Blackbird host nests? Animal Behaviour 55(5): 1181–1189.

Colon, M. R., A. M. Long, and M. L. Morrison. 2017. Responses of an endangered songbird to an extreme drought event. Southeastern Naturalist, 16(2): 195–214.

Conkling, T. J., T. L. Pope, K. N. Smith, H. A. Mathewson, M. L. Morrison, R. N. Wilkins, and J. W. Cain III. 2012. Black-capped Vireo nest predator assemblage and predictors for nest predation. Journal of Wildlife Management 76(7): 1401–1411.

Dawson, A. 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starlings *Sturnus vulgaris*. Ibis 146:493–500.

Dawson, A., S. A. Hinsley, P. N. Ferns, R. H. C. Bonser, and L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproduction to future survival. Proceedings of the Royal Society of London Series B 267:2093–2098.

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9(6): 1380–1395.

Fonteyn, P. J., M. W. Stone, M. A. Yancy, J. T. Baccus, and N. M. Nadkarni. 1988.
Determination of community structure by fire. Pages 79–90 in B. B. Amos and F.
R. Gehlbach, editors. Edwards Plateau vegetation: plant ecological studies in
central Texas. Baylor University Press, Waco, Texas, USA.

Fu, Y. S. H., X. Zhang, S. L. Piao, F. H. Hao, X. J. Geng, Y. Vitasse, C. Zohner, J.
Penuelas, and I. A. Janssens. 2019. Daylength helps temperate deciduous trees to
leaf-out at the optimal time. Global Change Biology 25(7): 2410–2418.

Gilman, E. F., and D. G. Watson. 1993. *Juniperus ashei*: Ashe Juniper. US Forest Service
Fact Sheet ST-321. USDA, Washington, DC. Available online at
<https://hort.ifas.ufl.edu/database/documents/pdf/tree_fact_sheets/junasha.pdf>.
Accessed 14 December 2022.

Gonzalez-Rojas, J. I., C. C. Farquhar, M. Guerrero-Madriles, O. Ballesteros-Medrano,
and A. Nunez-Gonzali. 2014. Breeding records of Black-capped Vireo (*Vireo
atricapilla*) in Northeastern Mexico. Wilson Journal of Ornithology, 126(1): 151–
155.

Graber, J. W. 1957. A bioecological study of the Black-capped Vireo (*Vireo atricapilla*).
Phd Thesis, Univ. of Oklahoma, Norman.

Graber, J.W. 1961. Distribution, habitat requirements and life history of the Black-capped
Vireo (*Vireo atricapilla*). Ecological Monographs 31:313–336.

Grzybowski, J. A., D. J. Tazik and G. D. Schnell. 1994. Regional analysis of Black-
capped Vireo breeding habitats. Condor 96:512–544.

Grzybowski, J. A. 2020. Black-capped Vireo (*Vireo atricapilla*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi-org.libproxy.txstate.edu/10.2173/bow.bkcvir1.01>

Grzybowski, J. A., R. B. Clapp, and J. T. Marshall. 1986. History and current status of the Black-capped Vireo in Oklahoma. American Birds 40(5):1151–1161.

Harris, J., Smith, L., and S. McMurry. 2021. Fine-scale plasticity in nest placement can compensate for poor quality junipers as nesting trees for Gray Vireos. PeerJ 9:e12477 DOI 10.7717/peerj.12477

Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecological Monographs 56(3): 201–220.

Jackson, R. B., L. A. Moore, W. A. Hoffmann, W. T. Pockman, and C. R. Linder. 1999. Ecosystem rooting depth determined with caves and DNA. Proceedings of the National Academy of Science 96: 11387–11392.

Kostecke, R. M., S. G. Summers, G. H. Eckrich, and D. A. Cimprich. 2005. Effects of Brown-headed Cowbird (*Molothrus ater*) removal on Black-capped Vireo (*Vireo atricapilla*) nest success and population growth at Fort Hood, Texas. Ornithological Monographs 57: 28–37.

Kovar, D. G., J. H. Sperry, and D. A. Cimprich. 2018. Comparative reproductive ecology of co-occurring rare and common Vireos in shrublands and woodlands. Wilson Journal of Ornithology 130(2):410–426.

Liebezeit J. R., and T. L. George. 2002. Nest predators, nest-site selection, and nesting success of the dusky flycatcher in a managed ponderosa pine forest. Condor 104:507–517.

Martin, T. E. and G. R. Geupel. 1993. Nest-monitoring plots – methods for locating nests and monitoring success. Journal of Field Ornithology 64(4): 507-519.

Morrison, M. L. and A. Averill-Murray. 2002. Evaluating the efficacy of manipulating cowbird parasitism on host nesting success. Southwestern Naturalist 47(2): 236–243.

Mullin, S. J., and R. J. Cooper. 1998. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*) - visual stimuli facilitate location of arboreal prey. American Midland Naturalist 140(2): 397–401.

Nilsson, J.-Å., and E. Svensson. 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. Proceedings of the Royal Society of London Series B 263: 711–714.

Noa, L. A., D. A. Hirth, T. M. Donovan, and D. Cimprich. 2007. Demographic differences of Black-capped Vireos in 2 habitat types in central Texas. Journal of Wildlife Management 71(4): 1042–1049.

Pease, C. M., and J. A. Grzybowski. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. Auk 112(2): 343-363.

Pulliam, H.P. 1988. Sources, sinks, and population regulation. American Naturalist 132: 652–661.

Robinson, W. D., and T. R. Robinson. 2001. Is host activity necessary to elicit brood

> parasitism by cowbirds? Ethology, Ecology & Evolution 13(2): 161–171.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a

> comparison of recently developed methods that can be implemented in MARK

> and SAS. Animal Biodiversity and Conservation 27:187–205.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary

> traps. Trends in Ecology and Evolution 17(10): 474-480.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

Sharp, B. L. and B. E. Kus. 2006. Factors influencing the incidence of cowbird parasitism

> of Least Bell's Vireos. Journal of Wildlife Management 70(3): 682–690.

Sibole, T., Green, and M. C. 2009. Assessment of late season nesting by black-capped

> vireos in response to brown-headed cowbird parasitism. Final Report to U.S.

> Army Corps of Engineers, Fort Hood, Texas.

Smith-Hicks, K. N., T. J. Conkling, M. L. Morrison, J. W. Cain III, and R. N. Wilkins.

> 2017. Nest height and vertical vegetation associated with Black-capped Vireo

> breeding success in Southwest Texas. Southeastern Naturalist 16(4): 567–583.

Sperry, J. H., R. G. Peak, D. A. Cimprich, and P. J. Weatherhead. 2008. Snake activity

> affects seasonal variation in nest predation risk for birds. Journal of Avian

> Biology 39: 379–383.

Tazik, D. J. 1991. Proactive management of an endangered species on army lands: the

> Black-capped Vireo on the lands of Fort Hood, Texas. Phd Thesis, Univ. of

> Illinois, Urbana-Champaign.

Tazik, D. J., J. A. Grzybowski, and J. D. Cornelius. 1993. Status of the Black-capped

    Vireo at Fort Hood, Texas. Technical Report EN-94/01, Volume II. US Army

    Corps of Engineers Construction and Engineering Research Laboratories,

    Champaign, IL.

Texas Parks and Wildlife Department. [online]. 2020. Interpretive guide to Kickapoo

    Cavern State Park.

    <https://tpwd.texas.gov/publications/pwdpubs/media/pwd_br_p4501_0147d.pdf>

    (8 February 2023).

United States National Phenology Network. [online]. 2023. NPN visualization tool: daily

    spring index leaf anomaly. <https://www.usanpn.org/data/visualizations> (9

    February 2023).

U.S. Fish and Wildlife Service. 2016. Species status assessment for the Black-capped

    Vireo (*Vireo atricapilla*). Arlington Ecological Services Field Office, Arlington,

    Texas.

U.S. Fish and Wildlife Service. 2018. Post-delisting monitoring plan for the Black-

    capped Vireo (*Vireo atricapilla*). Arlington Ecological Services Field Office,

    Arlington, Texas.

Walker, L. E., J. M. Marzluff, and D. A. Cimprich. 2016. Source-sink population

    dynamics by a brood parasite: A case study of an endangered songbird, the Black-

    capped Vireo. Biological Conservation 203: 108-118.

Ward, D. and J. N. M. Smith. 2000. Brown-headed Cowbird parasitism results in a sink

    population in Warbling Vireos. Auk. 117(2): 337–344.

Weldon, A. J., and N. M. Haddad. 2005. The effects of patch shape on Indigo Buntings:

evidence for an ecological trap. Ecological Society of America 86(6): 1422-1431.