DO ATTRIBUTES OF GRAY VIREO NEST SITES INFLUENCE BROWN-HEADED COWBIRD BROOD PARASITISM?

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ABSTRACT: Brood parasitism can have major detrimental effects on the fitness of reproducing songbirds and often contributes to nest failure. As the Gray Vireo (*Vireo vicinior*) suffers high rates of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*), we hypothesized that vireos might choose nest sites selectively to thwart cowbird parasitism. To investigate this question, we measured and compared vegetative and spatial attributes of nest sites in a known breeding population of the Gray Vireo on the Sevilleta National Wildlife Refuge, New Mexico, in 2017 and 2018. Specifically, we compared parasitized and unparasitized nests with respect to the nest's height and the average height, diameter, and foliage density of the nest tree. We also compared the spatial attributes of the nearest neighboring nest, nearest parasitized nest, and the density of surrounding juniper trees within 50 m of a nest. Interestingly, among none of the variables measured did we find an association with the incidence of brood parasitism, suggesting that nest parasitism might be more strongly linked to other larger-scale ecological or behavioral variables.

The Gray Vireo (*Vireo vicinior*) breeds in the southwestern United States and northwestern Mexico and winters primarily in parts of northern Mexico, southern Arizona, and western Texas (Barlow et al. 1999). It has been categorized as "threatened" in New Mexico (NMDGF 2018) and is of conservation concern throughout its range (USFWS 2008, Rosenberg et al. 2016, Hargrove and Unitt 2017). During the breeding season, vireo pairs build nests in trees or shrubs, in New Mexico usually in One-seed Juniper (*Juniperus monosperma*) trees, and defend their breeding territory (Fischer 2020, Harris et al. 2020). After a 12- to 17-day incubation period and another 12- to 16-day nestling period, fledglings depart the nest (Barlow et al. 1999, Corman and Wise-Gervais 2005, Hargrove and Unitt 2017). DeLong and Williams (2006) reported an overall nest-success rate in New Mexico of ~33%, and Fischer (2020) reported a nest-success rate of ~25% in the Sevilleta National Wildlife Refuge (in the same population we studied). Factors depressing this rate are nest predation and brood parasitism by the Brown-headed Cowbird (*Molothrus ater*). Cowbird parasitism is a persistent problem the Gray Vireo faces throughout its breeding range. Parasitism by the cowbird reduces the host's fitness; for small birds rejecting the cowbird egg entails deserting the nest, and accepting the egg usually entails death of all the host's nestlings (Payne 1977). In some cases more than 50% of the failures of Gray Vireo nests have been attributed to a very high rate of nest abandonment following parasitism (DeLong and Williams 2006, Fischer 2020). Although the Gray Vireo prefers certain attributes when selecting nest sites in New Mexico (Harris et al. 2020), it is not known if these preferences, among others, impart defenses against

known reproductive stressors such as nest predation or parasitism (Payne 1977, Kus et al. 2008). Further information on the interaction between the vireo's nesting habitat and reproductive stressors such as brood parasitism is critical to a better understanding of the conservation needs of this species.

A number of factors may influence the cowbird's selection of breeding habitat, such as landscape features (Brittingham and Temple 1996, Tewksbury et al. 1997, Chace 2004), vegetation type (Tewksbury et al. 1997, Chace 2004), females' movement patterns (Rothstein et al. 1984), and the cowbird's population density in preferred edge habitats (Jensen and Cully 2005). While the cowbird's selection of breeding habitat has been well studied, the specifics of hosts' susceptibility and defense against parasitism, especially in regards to nest-site attributes and proximity of conspecific hosts, have received less attention. As a defense against parasitism, some avian hosts might select nest sites that are less vulnerable both in terms of the site's attributes that may aid in nest concealment, such as nest height (Brodhead et al. 2007), as well as spatial characteristics, such as distance to the next nearest nest (Clark and Robertson 1979, Burhans 1997). Since attributes of a bird's nest location and placement can be important defenses against parasitism (Rothstein 1975, Feeney et al. 2012), further study of whether vireos use this kind of defense was warranted. Although the importance of a host's nest-site defenses has been studied in some other commonly parasitized host species (Clotfelter 1998, Brodhead et al. 2007), it had not been investigated in the Gray Vireo.

In this study, we examined whether attributes of a Gray Vireo's nest site influence the probability of brood parasitism. Specifically, we compared brood parasitism in vireo nests with respect to nest height and the height, diameter, and density of nest trees—all attributes that have been shown to be influential to various degrees in songbirds' nest-site preference (Bailey and Thompson 2007, Purcell 2007, Krause and Schrader 2016, Harris et al. 2020). On the basis of past findings (Larison et al. 1998, Brodhead et al. 2007, Fiorini et al. 2009), we predicted that vireo nests located higher, in taller, wider, and more densely foliaged trees should be less likely to be parasitized, as these attributes should improve nest concealment (Caccamise 1977, Holway 1991, Burhans 1997, Powell and Steidl 2000). We also used GIS data to investigate whether or not a vireo nest's placement affects its probability of being parasitized, comparing this probability with respect to distance to nearest neighboring nest, distance to nearest parasitized nest, and number of juniper trees within 50 m of the nest. On the basis of previous studies, we hypothesized that nests whose closest neighbors were parasitized should have a higher probability of being parasitized themselves than those nests whose closest neighbors were not parasitized (Clotfelter 1998, Saunders et al. 2003). Additionally, following these same studies, we hypothesized that nests more distant from their neighbors should be less likely to be parasitized than those closer together. Finally, we hypothesized that the prevalence of brood parasitism of vireo nests should be inversely related to juniper density—or the number of trees around the nest tree itself—because of the cowbird's preference for more open, edge habitats (Brittingham and Temple 1983). Brood parasitism creates a significant strain on the Gray Vireo's reproduction (DeLong and Williams 2006), and better understanding of the factors contributing to it will broaden current knowledge of the vireo's natural history, ecology, and conservation.

METHODS

Study Site

Our study took place from May to August in 2017 and 2018 at the Sevilleta National Wildlife Refuge (NWR), in central New Mexico (Figure 1). Specifically, we focused on the juniper savannas and piñon–juniper forests of Los Pinos Mountains, on the eastern side of the refuge (see Stevens and Fischer 2018, Fischer 2020).

Attributes of Nest Locations and Nest Trees

We monitored 84 vireo nests on the refuge as part of a larger study of the vireo's demography and migration (n = 33 from 2018, n = 51 from 2017). Across both years, four of these nests had to be excluded from our analysis because of uncertainty whether they were parasitized or observations conflicted, leading to a total of 80 usable nests (n = 30 from 2018, n = 50 from 2017). We also included parasitism data from 36 similarly monitored nests found in 2016, using them only in generating an average rate of brood parasitism on the refuge, for comparison and reference. Additionally, in 2017 and 2018, we calculated the rate at which nests were depredated. We found nests by standard search methods (Martin and Geupel 1993) and by tracking adult female vireos equipped for radio telemetry. Once we located a nest, we recorded its GPS coordinates and elevation and, using a mirror pole, monitored it for parasitism every two to four days.

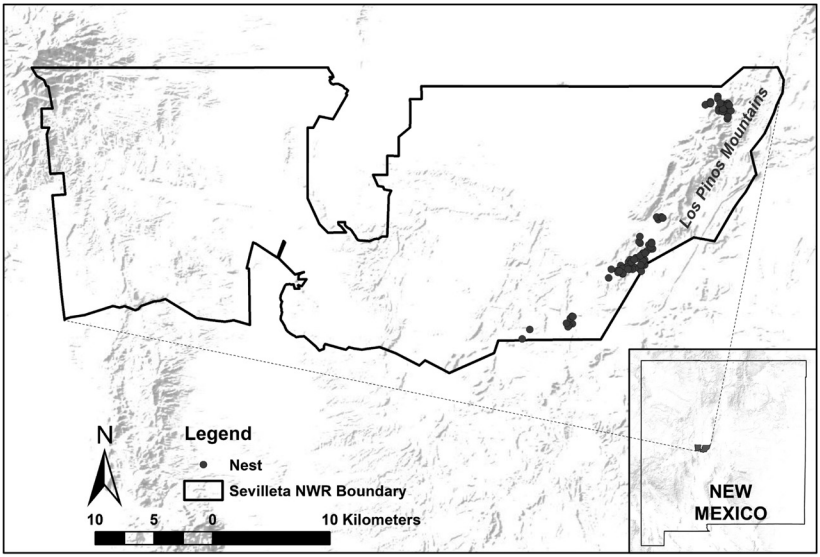

FIGURE 1. Sevilleta National Wildlife Refuge, New Mexico. The black dots represent the nest sites we studied within the refuge's part of Los Pinos Mountains.

To measure the average vegetative density of the nest tree, we used a 1-m × 1-m square board of 10-cm checkerboard tiles, held vertically at a fixed height on one side of the tree, while an observer stood on the opposite side of the tree and estimated the percent of the board covered by the tree's foliage. We then repeated the procedure on the opposite side of the tree and averaged the results to obtain one value for the nest tree's density. We used a marked PVC pole to measure the height of each nest from the ground and the nest tree's height and average diameter. Last, we took a compass bearing directly from the nest.

As a basis for comparing the spatial characteristics of nests, we quantified the distances among nest trees in the study area with ArcGIS software (version 3.2.0). To calculate the density of junipers, we defined a circle of radius 50 m around each nest tree and counted the number of junipers within that radius in ArcGIS. To account for observer error, two observers counted independently and averaged their counts. We used the standard distance tools in the software to measure the distance from each vireo nest to the nearest neighboring nest and nearest parasitized nest.

Statistical Analyses

We used program *R* (version 3.5.0) for our statistical analyses of the 80 nests for which we had adequate data in 2017 and 2018. We used two-sample, two-tailed Welch's *t*-tests to test whether or not a nest was parasitized against the measured variables, including nest height from ground and the nest tree's height, average vegetative density, and average diameter. We used the same methods to test whether or not the distance variables, distance to nearest neighboring nest, distance to nearest parasitized nest, and juniper density within a 50-m radius could explain the incidence of brood parasitism. We set $\alpha = 0.05$ for all comparisons.

RESULTS

The incidence of parasitism of vireo nests on the Sevilleta NWR was 28% in 2016, 50% in 2017, and 50% in 2018 ($n = 116$), for an average rate across all years of 43%. Rates of depredation of vireo nests were 50% in 2017 and 20% in 2018 ($n = 80$), for an average rate of 39% across both years. Among the nests monitored across all three years, only one fledged a single juvenile cowbird, entailing death of the vireo nestlings. As was expected in the Gray Vireo, all other incidences of parasitism resulted in complete nest abandonment, regardless of stage. While parasitism almost always resulted in abandonment, some instances of predation did not, leading to some nests being both parasitized and depredated. All 116 nests found from 2016 to 2018 were in One-seed Juniper trees.

The unparasitized and parasitized vireo nests did not appear to differ in any of the vegetative and spatial characteristics we measured. The differences were not statistically significant in the comparisons of the nest's height ($p = 0.818$, $t = -0.231$, df = 64.11), the nest tree's height ($p = 0.730$, $t = 0.347$, df = 54.76), the nest tree's diameter ($p = 0.665$, $t = 0.4355$, df = 57.92), or the nest tree's vegetative density ($p = 0.243$, $t = -1.180$, df = 55.17; Figure 2). Neither did the mean distance to the nearest neighboring nest ($p = 0.579$, $t = 0.557$,

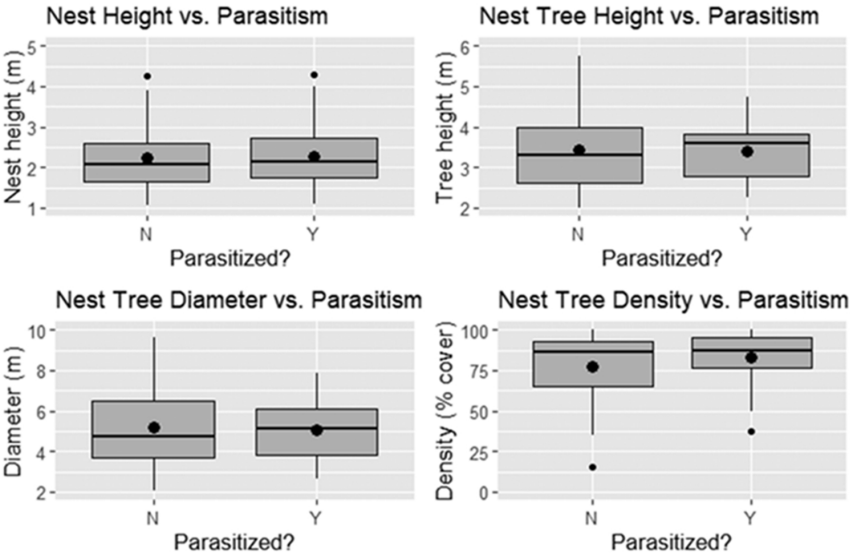

Figure 2. Box plots comparing four attributes of Gray Vireo nest sites (nest height and the nest tree's height, average diameter, and average density) by incidence of Brown-headed Cowbird brood parasitism. In the boxplots, black circles within boxes represent means, heavy central lines represent medians, darker gray boxes represent the interquartile range, whiskers represent the extremities of the data, and dots beyond whiskers represent any outliers for each category. Data are from 2017 and 2018 with a sample size of $n = 80$.

df = 59.51) or the nearest parasitized nest ($p = 0.171$, $t = 1.385$, df = 64.82) differ significantly. Finally, the density of the stands of junipers within 50 m surrounding the nest had no association with the rate of cowbird parasitism on vireo nests ($p = 0.557$, $t = -0.591$, df = 60.43).

DISCUSSION

Multiple studies have confirmed that brood parasitism is a persistent reproductive challenge for the Gray Vireo in New Mexico (DeLong and Williams 2006, Pierce 2007, Harris et al. 2020), and this is true on the Sevilleta NWR as well. The average parasitism rate of 43% we found over three years among 116 nests, while slightly lower than the 50% average previously reported for New Mexico vireos, is still well within the 24–71% others have found for the region (Delong and Williams 2006, Pierce 2007).

Our finding no association of the incidence of cowbird parasitism with the attributes we evaluated, either vegetative and spatial, suggests that other, larger-scale environmental or behavioral variables beyond the nest site might better explain susceptibility to parasitism. These could include the density of cowbirds, distance to cattle or other livestock, and aspects of the vireo's nesting behavior such as males singing conspicuously while incubating. Goguen

and Matthews (2000) reported that differences in rates of cowbird parasitism of nests of the Plumbeous Vireo (*Vireo plumbeus*) could be attributed to changes in patterns of nearby livestock grazing. Goguen and Matthews (2001) found proximity to livestock to be the main factor affecting cowbird densities and the probability of a nest's being parasitized. With respect to the cowbird's density-dependence, Brittingham and Temple (1983) showed that in areas with more cowbirds, songbirds simply tend to have higher rates of brood parasitism. In our study, we did not record specific data on cowbird abundance or larger landscape-scale variables such as the distance to livestock herds, but we suspect that these studies' results could apply to the Gray Vireo at the Sevilleta NWR as well.

Our results imply that the variables we studied may not be as vital for the Gray Vireo in selecting a nest site to defend against cowbird parasitism. Although variables such as a nest's exposure and proximity of perches have been suggested as factors contributing brood parasitism (Fiorini et al. 2009, Feeney et al. 2012), our results suggest that other, unstudied attributes are more important. Future studies of cowbird parasitism of the Gray Vireo might examine average temperature of the nest site, geographic aspect, territory size, distance to water, and additional vegetation variables, as well as the aforementioned distance to cattle herds or edge habitats.

CONCLUSION

Cowbird parasitism is a threat to the fitness and population demographics of songbirds like the Gray Vireo. With the vireo classified as "threatened" in New Mexico, and meriting such designation in other parts of its range, understanding this parasitic relationship and the environmental variables affecting its incidence is vital for conserving this species. Our results suggest that the vireo might not in fact be engaging in certain nest-defense strategies, potentially increasing its vulnerability to parasitism. We hope our results will aid future studies that focus on the factors most critical to conservation of the Gray Vireo.

ACKNOWLEDGMENTS

We thank the National Science Foundation and the Sevilleta long-term ecological research program through the University of New Mexico for supporting and funding our research. We thank Stephanie Baker, Alesia Hallmark, Ben Specter, and Scott Collins for supporting our research, and the Research Experience for Undergraduates program at the Sevilleta NWR. We also thank Henry Streby at University of Toledo for helping oversee the larger demographic study of the Gray Vireo at the Sevilleta NWR. Thank you to Ethan Clotfelter and Daniel D. Gibson for their reviews of the manuscript.

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Accepted 22 November 2021
Associate editor: Matthew J. Baumann

Gray Vireo (*Vireo vicinior*) on nest, Sevilleta National Wildlife Refuge, New Mexico, 9 June 2020.

Photo by Silas E. Fischer