

## UNDERSTANDING NEST SUCCESS AND BROOD PARASITISM IN THE ENDANGERED BLACK-CAPPED VIREO: COMPARISONS WITH TWO SYMPATRIC SONGBIRDS

ANDREW J. CAMPOMIZZI,<sup>1,7</sup> HEATHER A. MATHEWSON,<sup>1</sup> MICHAEL L. MORRISON,<sup>2</sup> CHRISTOPHER M. LITUMA,<sup>2,3</sup> TARA J. CONKLING,<sup>2,4</sup> M. CONSTANZA COCIMANO,<sup>2</sup> SHANNON L. FARRELL,<sup>1</sup> R. NEAL WILKINS,<sup>1,5</sup> AND JERROD A. BUTCHER<sup>2,6</sup>

**ABSTRACT.**—Nest predation and brood parasitism likely cause declines in many songbird species, yet the rate of these declines varies among species. Simultaneously studying co-occurring species with overlapping territories provides an opportunity to identify differences among the species that may explain differential reproductive success. We monitored nests of three co-occurring songbird species to determine whether the federally endangered Black-capped Vireo (*Vireo atricapilla*) experienced lower reproductive success than Northern Cardinals (*Cardinalis cardinalis*) and White-eyed Vireos (*V. griseus*) on private lands with and without trapping of brood parasites. We assessed if habitat metrics and nesting phenology were associated with nest success and frequency of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) to determine if these characteristics explain poor reproductive success. We monitored 188 nests in shrubland and ecotones with woodlands in central Texas from 2006–2008. We found species-specific differences in nest success and brood parasitism, year effects, and differential impacts of cowbird trapping. Black-capped Vireos nesting in locations without cowbird trapping experienced the lowest daily survival rate of nests (0.86) and period nest survival (0.01), whereas estimates in locations with cowbird trapping were similar to the other species (0.93 for daily and 0.11 for period nest survival). Nest initiation date was important for predicting brood parasitism, showing high probability of brood parasitism in the middle of the breeding season and low probability during the beginning and end of the season. Habitat metrics were not good predictors of nest success or brood parasitism. Management for conservation of Black-capped Vireos focused on vegetation manipulation may not increase reproductive success in the absence of cowbird trapping in some areas of the breeding range, because daily survival rate of nests was associated with cowbird trapping but not habitat metrics. Received 7 March 2013. Accepted 2 August 2013.

**Key words:** brood parasitism, *Cardinalis cardinalis*, edge effect, *Molothrus ater*, nest survival, *Vireo atricapilla*.

Poor reproductive success is likely one of the primary causes of declines in many songbird species (Martin 1992, Peterjohn et al. 1995). Reproductive success is, in part, constrained by nest success and brood parasitism. These constraints can vary spatially, temporally, and among species. Many songbird species have low reproductive success (e.g., Nice 1957, Ricklefs 1969, Campomizzi et al. 2009) and high frequency of brood parasitism (e.g., Rothstein and Cook 2000, Farrell et al. 2010). Comparisons among co-

occurring songbirds, with overlapping territories, exposed to similar risks may elucidate if and reasons why one species may experience low reproductive success compared to other species. Understanding the conditions under which these constraints occur can inform the management of affected species.

The Black-capped Vireo (*Vireo atricapilla*) is a species of conservation concern and co-occurs with White-eyed Vireos (*V. griseus*) and Northern Cardinals (*Cardinalis cardinalis*). Low reproductive success led to concerns that the Black-capped Vireo population was declining, and this was a primary factor for listing them as endangered (USFWS 1991). Previous studies have documented low reproductive success (Kostecke et al. 2005, Campomizzi et al. 2009) and high frequency of brood parasitism (Kostecke et al. 2005, Farrell et al. 2010). The majority of published research about Black-capped Vireos comes from public properties, particularly Fort Hood military base, which has intensive conservation programs that include vegetation restoration and removal of brood parasites (Kostecke et al. 2005; Summers et

<sup>1</sup> Institute of Renewable Natural Resources, Texas A&M University, College Station, TX, USA.

<sup>2</sup> Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX, USA.

<sup>3</sup> Current address: Forestry, Wildlife and Fisheries, University of Tennessee, Knoxville, TN, USA.

<sup>4</sup> Current address: Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, MS, USA.

<sup>5</sup> Current address: East Wildlife Foundation, 200 Concord Plaza, Suite 410, San Antonio, TX, USA.

<sup>6</sup> Current address: Alvin Community College, 3110 Mustang Road, Alvin, TX, USA.

<sup>7</sup> Corresponding author;  
e-mail: acampomizzi@gmail.com

al. 2006a, b; Noa et al. 2007). Research has also occurred on other public properties (e.g., Balcones National Wildlife Refuge, Fort Sill military base, Kerr Wildlife Management Area, Wichita Mountains National Wildlife Refuge; Fazio et al. 2004, Barr et al. 2008, Zink et al. 2010, Pope et al. 2013). However, little is known about reproductive success throughout most of the breeding range because >90% of their breeding range occurs on private land (Wilkins et al. 2006, Campomizzi et al. 2009, Farrell et al. 2010, Conkling et al. 2012). Private lands have different land uses than public properties and most are not specifically managed for Black-capped Vireos through vegetation manipulation or removal of brood parasites, although there are conservation programs implemented on some private properties (e.g., Texas Parks and Wildlife Department's Landowner Incentive Program, Environmental Defense Fund's application of safe harbor agreements). Thus, knowledge from studies of reproductive success on public properties may not be applicable to private properties. We addressed this knowledge gap by focusing our research on private land with the understanding that Black-capped Vireos may be rare on private lands, limiting analytical options, but that the information would nevertheless be valuable to improve our understanding of their reproductive success on land ownership comprising the majority of their breeding range.

Nest predation is the most common cause of nest failure in many songbird species (Nice 1957, Ricklefs 1969, Martin 1993), including Black-capped Vireos (Stake and Cimprich 2003, Conkling et al. 2012). Rat snakes (*Elaphe* spp.), fire ants (*Solenopsis* spp.), and Brown-headed Cowbirds (*Molothrus ater*) have been identified as primary predators of nests of Black-capped Vireos in central Texas (Stake and Cimprich 2003, Campomizzi et al. 2009, Conkling et al. 2012). In addition to being a brood parasite, Brown-headed Cowbirds are considered nest predators, because they remove host eggs and nestlings, often causing nest failure. Relationships between nest predation and habitat metrics are complex (Lahti 2001, Chalfoun et al. 2002) and can be specific to the system and species studied.

Patterns of habitat use and abundance have been identified for nest predators of Black-capped Vireos. Edges between woodland and non-woodland were preferred by rat snakes (Blouin-Demers and Weatherhead 2001a, b; Sperry 2008) and also

provide for increased activity and abundance of fire ants (Tschinkel 1987, Stiles and Jones 1998) and Brown-headed Cowbirds (Brittingham and Temple 1983, Paton 1994, Howell et al. 2007). Additionally, increases in the proportion of woody cover may lead to decreased predation by Brown-headed Cowbirds (Thompson 1994, Goguen and Mathews 2001), rat snakes, and fire ants (Summerlin et al. 1976, Porter et al. 1988, Porter and Savignano 1990, Stein et al. 1990, Stiles and Jones 1998). Lastly, nest predator activity increased as the season progressed for snakes (Sperry et al. 2008, Sperry and Weatherhead 2008), Brown-headed Cowbirds (Burhans and Thompson 1998), and fire ants (Stein et al. 1990).

Brood parasitism reduces reproductive success in some species (Rothstein and Peer 2005), particularly in Black-capped Vireos (Kostecke et al. 2005, Farrell et al. 2010). As with nest predation, relationships between frequency of parasitism and habitat metrics vary among studies and systems (Paton 1994, Gustafson et al. 2002, Sharp and Kus 2006, Howell et al. 2007). Patterns of cowbird occurrence and parasitism frequency have been described. Brown-headed Cowbirds can be more common near edges between woodland and non-woodland (Brittingham and Temple 1983, Paton 1994, Howell et al. 2007) and landscapes with more woody cover can have lower frequency of parasitism (Brittingham and Temple 1983). Areas with little woody cover may function similar to edges for cowbirds. Additionally, parasitism frequency can be low early in the breeding season, gradually increase to a mid-season peak, and then decrease at the end of the season (Briskie et al. 1990, Woodworth 1999, Hoover et al. 2006). However, the timing of cowbird egg-laying might more closely correspond to the nest initiation date of a particular host species, making one host species more susceptible to parasitism than another host species.

Our objective was to study nest success and brood parasitism in the Black-capped Vireo (*Vireo atricapilla*) to improve our understanding of its reproductive success through comparisons with White-eyed Vireos and Northern Cardinals on private lands in central Texas with and without management for cowbirds. We used comparisons with co-occurring songbirds with overlapping territories exposed to similar risks to investigate if and reasons why Black-capped Vireos may experience low reproductive success. All three

species build open-cup nests, are in the order Passeriformes, and are parasitized by Brown-headed Cowbirds. Although many possible factors could influence differential reproductive success among these species, we investigated broad-level characteristics of the habitat that are likely to influence nest success and brood parasitism based on the ecology of nest predators and brood parasites. We hypothesized (1) Black-capped Vireos would have lower reproductive success as a consequence of lower daily survival rate of nests or longer nesting period (from egg-laying to fledging offspring) compared with the other two species, (2) habitat metrics (woody cover, edge density) around nests of Black-capped Vireos at two spatial scales would be associated with lower reproductive success and greater frequency of brood parasitism by Brown-headed Cowbirds compared to the other two species, and (3) nest initiation date and ordinal date of season for Black-capped Vireo would be associated with time periods of the breeding season with higher parasitism frequency and lower daily survival rate of nests, respectively, compared to the other two species.

## METHODS

**Study Area.**—We conducted this study in the Leon River watershed in central Texas. The study area was within the Limestone Cut Plain level IV eco-region in the Cross Timbers level III eco-region, consisting of broad valleys between mesas on Lower Cretaceous limestone (Griffith et al. 2004). Vegetation where we monitored nests consisted of mid-successional stage shrubland similar to nearby areas previously used for research on Black-capped Vireos (Grzybowski et al. 1994, Bailey and Thompson 2007), ecotones between oak-juniper (*Quercus-Juniperus*) woodland and grassland, and adjacent oak-juniper woodland. The most common species of woody vegetation were oaks, juniper, eastern redbud (*Cercis canadensis*), elbow bush (*Forestiera angustifolia*), and Texas ash (*Fraxinus albicans*). We monitored nests on mesa tops and slopes on the sides of mesas. Elevation in the study area ranged from 200–500 m. We visited privately owned properties that experienced similar disturbance and land management practices typical of the study area including ranching, hunting, and agriculture. We detected Black-capped Vireos in 10 locations during initial surveys on 33 properties within a 140,000-ha area. Locations had 36–

103-ha patches of vegetation where we searched for nests. We monitored nests at all 10 locations annually unless Black-capped Vireos were not nesting in a location or we no longer could obtain permission to access properties. Cowbird trapping was conducted during each year with 30–40 traps distributed among five of the nest monitoring locations. A contractor replenished food and water in traps once every two days when temperature was  $<30^{\circ}\text{C}$ , daily when  $\geq 30^{\circ}\text{C}$ , and euthanized cowbirds by cervical dislocation.

**Nest Monitoring.**—We searched for nests using behavioral cues and systematic searching (Martin and Geupel 1993) from 15 March to 31 July in 2006–2008 for Black-capped Vireos and White-eyed Vireos, and in 2006 and 2007 for Northern Cardinals. We checked active nests every 3–4 days to record nest contents including host eggs, cowbird eggs, number of young, and age of young. We estimated the age of young based on their size, feather development, and behavior (Grzybowski 1995, Hopp et al. 1995). We recorded the date each nest was found and, based on successive checks, either observed when the first host egg was laid in each nest or back-dated nests to estimate nest initiation date for nests found after eggs were laid (Mayfield 1975).

We considered a nest successful if  $\geq 1$  host young fledged from the nest. We determined fledging by observations of adults carrying food to fledglings or detection of fledglings by sight or sound near nests that had large nestlings near fledging age on our previous nest check. We considered nests failed if they were empty after having eggs or if we did not detect fledglings or observe adults carrying food near nests that previously had nestlings. Nests that were abandoned by adults in the absence of a partial predation event were excluded from our analyses, because we were unable to determine when the nest became inactive; nest abandonment was rare for all three species. We recorded the location of each nest to  $\sim 6\text{-m}$  accuracy using a hand-held global positioning system (GPS).

**Habitat Metrics.**—We used habitat metrics likely to influence daily survival rate and brood parasitism of nests based on the ecology of nest predators and brood parasites. Our metrics of interest were edge density and woody cover within 100-m and 500-m radii from the nest. We used two spatial scales, because the importance of investigating the relationship between predictor variables and daily survival rate of nests at

TABLE 1. Evaluation of logistic exposure models for predicting daily survival rate of nests of Black-capped Vireos ( $n = 38$ ), Northern Cardinals ( $n = 97$ ), and White-eyed Vireos ( $n = 53$ ) monitored from 2006–2008 in central Texas. Interactions are designated with an asterisk and include additive effects of variables in interaction.

| Model <sup>a</sup>           | K <sup>b</sup> | AIC <sub>c</sub> <sup>c</sup> | $\Delta$ AIC <sub>c</sub> <sup>d</sup> | $w_i$ <sup>e</sup> | –2 log likelihood |
|------------------------------|----------------|-------------------------------|----------------------------------------|--------------------|-------------------|
| species * year               | 8              | 709.96                        | 0.00                                   | 0.57               | –346.87           |
| species * trap               | 6              | 711.61                        | 1.65                                   | 0.25               | –349.74           |
| species                      | 3              | 713.70                        | 3.73                                   | 0.09               | –353.83           |
| intercept                    | 1              | 714.90                        | 4.93                                   | 0.05               | –356.44           |
| species * woody cover        | 6              | 717.97                        | 8.01                                   | 0.01               | –352.92           |
| species * edge + trap        | 7              | 718.27                        | 8.30                                   | 0.01               | –352.05           |
| species * edge               | 6              | 718.88                        | 8.92                                   | 0.01               | –353.37           |
| species * date               | 6              | 719.06                        | 9.09                                   | 0.01               | –353.46           |
| species * woody cover + trap | 7              | 719.23                        | 9.26                                   | 0.01               | –352.53           |
| species * date + trap        | 7              | 719.83                        | 9.87                                   | 0.00               | –352.83           |

<sup>a</sup> Variables were: species = 3 species studied, trap = trapping for Brown-headed Cowbirds, edge density = density of edge in woody vegetation (m/m<sup>2</sup>) within 500 m of nests, woody cover = proportion of woody vegetation within 500 m of nest, date = ordinal date of season, year = year nest was active.

<sup>b</sup> Number of parameters in each model.

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

<sup>d</sup> Difference in AIC<sub>c</sub> values compared to the best-fit model.

<sup>e</sup> Model weights.

multiple spatial scales is clear in the literature (Chalfoun et al. 2002, Stephens et al. 2003). Thus, we chose a 100-m radius because it exhibits characteristics occurring within a Black-capped Vireo's territory, which is typically 1–4 ha in Texas (Grzybowski 1995), and a 500-m radius because it represents a broader spatial context representative of the landscape through which nest predators and brood parasites move.

We used ArcMap™ 9.2 (ESRI®, Redlands, California, USA) to characterize vegetation within a 100-m and a 500-m radius centered at each nest. We used the ISO cluster and maximum likelihood classifier functions in Spatial Analyst to run an unsupervised classification of a 2005 National Agriculture Image Program (NAIP) aerial image with 2-m grain. We reclassified the unsupervised classification into two classes, woody cover and non-woody cover, for our analyses. We used the ArcMap extension Hawth's tools (available at [www.spatialecology.com](http://www.spatialecology.com)) to calculate the proportion of pixels classified as woody cover within each radius. We defined edge as the boundary between woody and non-woody vegetation classes and calculated edge density (edge m/area m<sup>2</sup>) at each spatial scale for each nest. We examined multicollinearity among spatial variables using a variance inflation factor >0.2 as a criterion for removal from the modeling process described below (Graham 2003). Woody cover and edge density were correlated between 100-m and 500-m radii (Black-capped Vireo  $r = 0.755$ , Northern

Cardinal  $r = 0.625$ , White-eyed Vireo  $r = 0.704$ ). Thus, we used data from the 500-m radii for analyzing daily survival rate of nests because it includes a bird's territory and surrounding landscape (i.e., the scale at which management is likely to occur).

**Nest Survival.**—We defined daily survival rate as the probability a nest would survive one day and period nest survival as the probability a nest would survive the entire nesting period from laying of the first egg to fledging young (estimated mean 30 days for Black-capped Vireos [Grzybowski 1995], 25 days for Northern Cardinals [Halkin and Linville 1999], and 27 days for White-eyed Vireos [Hopp et al. 1995]). We did not estimate length of nesting period using our data, because few nests of Black-capped Vireos survived the duration of the nesting period. We used ordinal date (i.e., from 1 Jan = 1 to 31 Dec = 365 or 366) to standardize date of season.

We used an information-theoretic approach to evaluate 10 *a priori* logistic exposure models (Shaffer 2004) that addressed differential daily survival rate of nests among our three study species (Table 1). We developed statistical models based on our research hypotheses in the introduction. We predicted that daily survival rate would vary among the three species, thus we considered a single-effects model for species-specific survival and models with an interaction to account for species-specific rela-

TABLE 2. Evaluation of logistic regression models for predicting probability of brood parasitism of nests of Black-capped Vireos ( $n = 38$ ), Northern Cardinals ( $n = 97$ ), and White-eyed Vireos ( $n = 53$ ) monitored from 2006–2008 in central Texas. Interactions are designated with an asterisk and include additive effects of variables in interaction.

| Model <sup>a</sup>                 | K <sup>b</sup> | AIC <sub>c</sub> <sup>c</sup> | $\Delta$ AIC <sub>c</sub> <sup>d</sup> | $w_i$ <sup>e</sup> | –2 log likelihood |
|------------------------------------|----------------|-------------------------------|----------------------------------------|--------------------|-------------------|
| species * quadratic date + trap    | 8              | 106.78                        | 0.00                                   | 0.82               | –44.89            |
| species * woody cover 500 m + trap | 7              | 112.07                        | 5.29                                   | 0.06               | –48.64            |
| species * edge 500 m + trap        | 7              | 112.92                        | 6.14                                   | 0.04               | –49.07            |
| species * woody cover 100 m + trap | 7              | 112.92                        | 6.14                                   | 0.04               | –49.07            |
| species * trap                     | 6              | 113.33                        | 6.55                                   | 0.03               | –50.37            |
| species * edge 100 m + trap        | 7              | 115.38                        | 8.59                                   | 0.01               | –50.30            |
| species * edge 100 m               | 6              | 150.03                        | 43.25                                  | 0.00               | –68.73            |
| species * edge 500 m               | 6              | 150.49                        | 43.71                                  | 0.00               | –68.96            |
| species * quadratic date           | 7              | 151.31                        | 44.53                                  | 0.00               | –68.27            |
| species                            | 3              | 153.76                        | 46.97                                  | 0.00               | –73.80            |
| species * woody cover 500 m        | 6              | 156.20                        | 49.42                                  | 0.00               | –71.81            |
| species * woody cover 100 m        | 6              | 157.45                        | 50.67                                  | 0.00               | –72.44            |
| intercept                          | 1              | 195.99                        | 89.20                                  | 0.00               | –96.98            |

<sup>a</sup> Variables were: species = 3 species studied, cowbird trap = trapping for Brown-headed Cowbirds, woody cover 100 m = proportion of woody vegetation within 100 m of nest, woody cover 500 m = proportion of woody vegetation within 500 m of nest, edge density 100 m = density of edge in woody vegetation (m/m<sup>2</sup>) within 100 m of nests, edge density 500 m = density of edge in woody vegetation (m/m<sup>2</sup>) within 500 m of nests, quadratic date = quadratic ordinal date when first host egg laid in nest.

<sup>b</sup> Number of parameters in each model.

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

<sup>d</sup> Difference in AIC<sub>c</sub> values compared to the best-fit model.

<sup>e</sup> Model weights.

tionships with habitat metrics and ordinal date. We included the additive effect of cowbird trapping to models because of the influence it has on the daily survival rate of nests. We included a model with an interactive effect of species and year because daily survival rate often varies among years. Lastly, we included an intercept-only model to compare model fit assuming a constant daily survival rate with models based on our hypotheses.

We used AIC<sub>c</sub> model selection (Akaike Information Criterion corrected for small sample size relative to the number of parameters in the model) to assess relative fit among candidate models (Burnham and Anderson 2002b). We considered models with  $\Delta$ AIC<sub>c</sub> < 2.0 to be competitive for the best model (Burnham and Anderson 2002a). We did not examine a goodness-of-fit of the best-fit model because of poor approximation of the sampling distribution when sample sizes are small, such as they are when including continuous covariates in our candidate models (Shaffer and Thompson 2007). We estimated daily survival rate using coefficients from competitive models. We estimated period nest survival by raising estimates of daily survival rate to the power of the number of days in the nesting period for each species to enable inter-specific comparisons of period nest survival. We used program R 2.15 (R

Development Core Team 2012) for conducting analyses and producing figures.

**Cowbird Parasitism.**—We considered a nest parasitized if we found an egg from a Brown-headed Cowbird in the host nest within 3 days of the first egg laid by the host; this timing enables cowbird eggs to hatch before or with host eggs. We used a similar approach to our analysis for nest survival. We evaluated 13 *a priori* logistic regression models that addressed differential brood parasitism among the three species based on our research hypotheses (Table 2). We included a single-effects model for species-specific parasitism and models with an interaction to account for species-specific relationships with habitat metrics and nest initiation date. We included the additive effect of cowbird trapping to models because of the influence it has on parasitism frequency. Lastly, we included the intercept-only model. We analyzed spatial variables at 100- and 500-m radii centered at each nest because we did not detect multicollinearity in this data set. We used the best-fit model to predict probability of brood parasitism.

## RESULTS

**Nest Survival.**—We monitored 188 nests of Black-capped Vireos ( $n = 38$ ), White-eyed Vireos ( $n = 53$ ), and Northern Cardinals ( $n =$

97). The best-fit model for daily nest survival was the interactive effect of species and year (Table 1). The interactive effect of species and cowbird trapping was also a competitive model ( $\Delta AIC_c = 1.65$ ; Table 1). Models including the proportion of woody cover, edge density, or ordinal date were not competitive (Table 1). Mean daily survival rate of nests was higher in 2008 for Black-capped and White-eyed vireos compared to 2006 and 2007 (Fig. 1). Mean daily survival rate of nests for Black-capped Vireos in locations without cowbird trapping was lower (0.86) and outside of 95% confidence intervals than estimates for Black-capped Vireos in locations with cowbird trapping and White-eyed Vireos and Northern Cardinals with and without cowbird trapping (Fig. 1). Period nest survival for Black-capped Vireos was higher in locations with cowbird trapping (0.11) than without trapping (0.01). Period nest survival for White-eyed Vireos was also higher in locations with trapping (0.23) compared to locations without trapping (0.07). In contrast, period nest survival of Northern Cardinals was lower in locations with trapping (0.09) than in locations without trapping (0.15).

**Cowbird Parasitism.**—Parasitism frequency was 72% for Black-capped Vireos, 6% for Northern Cardinals, and 30% for White-eyed Vireos. Observed median nest initiation date for Black-capped Vireos was 20 days later than Northern Cardinals and 15 days later than White-eyed Vireos. The best-fit model was the interactive effect of species with a quadratic effect of nest initiation date and the additive effect of cowbird trapping (Table 2). Models including proportion of woody cover and edge density within 100- and 500-m radii centered at each nest were not competitive (Table 2). The best-fit model predicted probability of parasitism as relatively low during the beginning and end of the breeding season and high during the middle of the breeding season, but with varying magnitudes depending on species and presence of cowbird trapping (Fig. 2). The greatest probability of brood parasitism was  $\sim 1.0$  for Black-capped Vireos during the middle of the breeding season in locations without cowbird trapping. Similarly, the probability of brood parasitism for White-eyed Vireos was about 0.8 during the middle of the breeding season without cowbird trapping, whereas for Northern Cardinals the probability did not exceed 0.4 (Fig. 2).

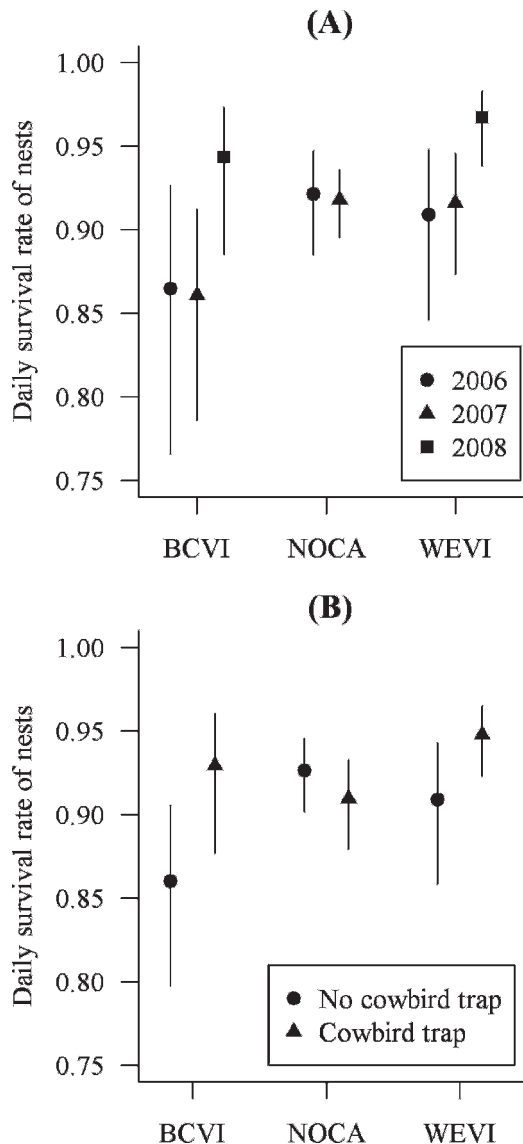


FIG. 1. Predicted daily nest survival rate of Black-capped Vireos (BCVI), Northern Cardinals (NOCA), and White-eyed Vireos (WEVI) based on the two competitive logistic exposure models, the interactive effect of species and year (A) and the interactive effect of species and cowbird trapping (B). We monitored nests ( $n = 188$ ) from 2006–2008 in central Texas (we did not monitor Northern Cardinal nests in 2008). Solid circles, triangles, and squares indicate predicted means and vertical lines indicate 95% confidence intervals.

Cowbird trapping reduced probability of parasitism to near zero for Northern Cardinals,  $<0.2$  for White-eyed Vireos, and  $<0.5$  for Black-capped Vireos (Fig. 2).

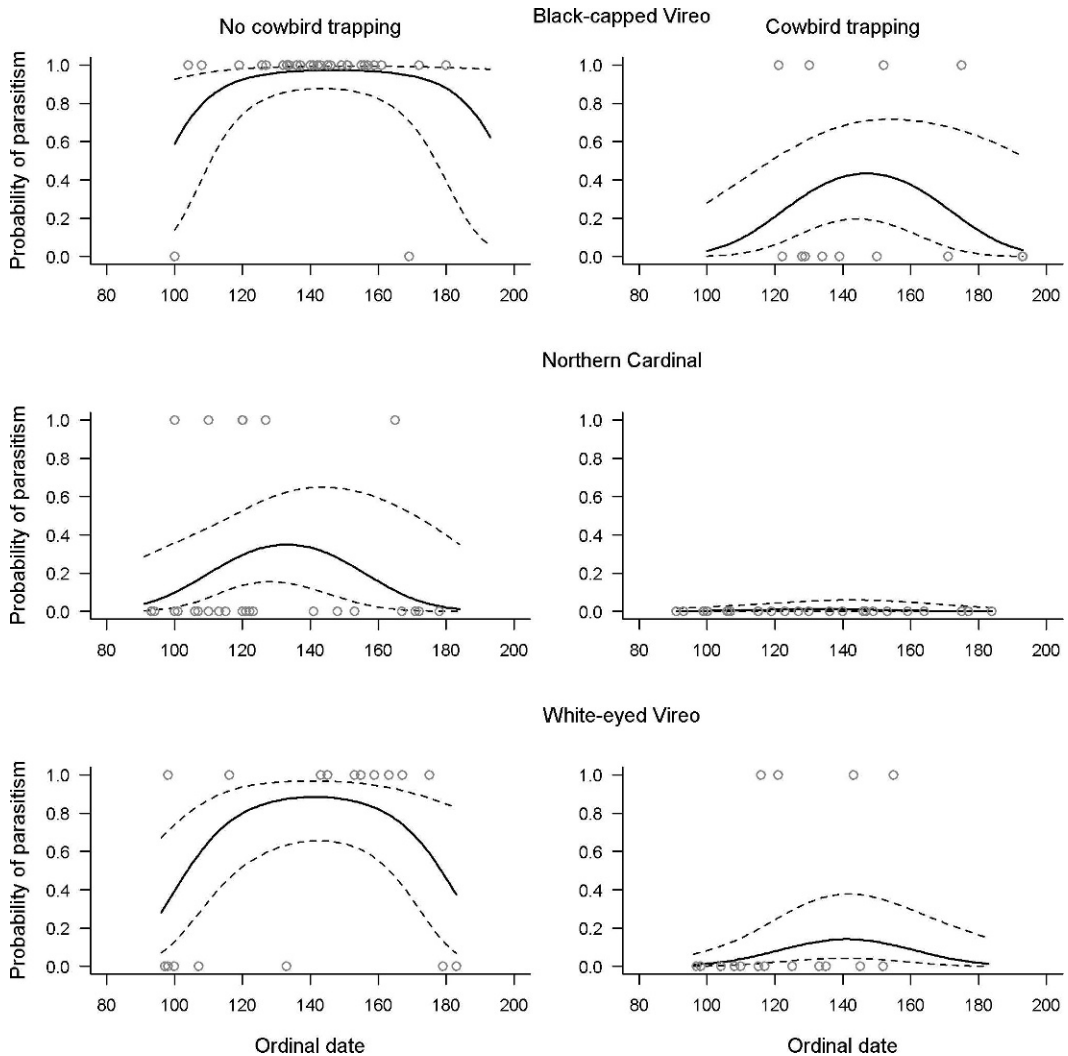


FIG. 2. Predicted probability of nest parasitism by Brown-headed Cowbirds on Black-capped Vireos, Northern Cardinals, and White-eyed Vireos during the range of ordinal nest initiation dates for each species. We used the best-fit logistic regression model (the interactive effect of species and a quadratic effect of nest initiation date and the additive effect of cowbird trapping) to predict probability of parasitism of a nest for each species based on our sample of nests ( $n = 188$ ) monitored from 2006–2008 in central Texas. Solid lines show predicted means, dashed lines 95% confidence intervals, and open circles observed data.

## DISCUSSION

Our study demonstrated species-specific differences in nest success and brood parasitism for three co-occurring songbirds. Additionally, nest success varied among years and removal of Brown-headed Cowbirds through trapping efforts differentially affected species. In locations without cowbird trapping, a combination of low daily survival rate of nests and a long nesting period led to low estimates of period nest survival for Black-capped

Vireos compared to the other species. Cowbird trapping increased daily survival rate of nests of Black-capped Vireos to estimates similar to the other species' daily survival rates regardless of cowbird trapping. Without the influence of cowbird trapping, both vireo species experienced high probabilities of brood parasitism; however, the magnitude of the reduction in parasitism from trapping was greater for White-eyed Vireos compared to Black-capped Vireos. Other studies

in patches of habitat of similar size have found similar estimates of daily survival rate for nests of Black-capped Vireos in areas with varying intensity of trapping for cowbirds (Kostecke et al. 2005, Campomizzi et al. 2009).

Contrary to our hypotheses based on the ecology of nest predators, habitat metrics (woody cover, edge density) did not produce competitive models of daily survival rate of nests. Based on previous research on other species, it is possible that particular characteristics of territories and vegetation characteristics at broader spatial extents could be associated with variation in daily survival rate (Thompson et al. 2002) or predator activity (Chalfoun et al. 2002). Similar to our results, previous research for songbirds indicated that reproductive success varies among years (e.g., Morrison and Averill-Murray 2002, Kostecke et al. 2005) and that cowbird trapping can increase reproductive success (Rothstein and Cook 2000). Additionally, the low reproductive success of Black-capped Vireos in our study, particularly in locations without cowbird trapping, could have indirect effects on adult survival (Butler et al. 2008).

Our results indicated Black-capped Vireos were more vulnerable to brood parasitism than the other two co-occurring species because they initiated nests later in the breeding season and possibly other species-specific differences. Although cowbird trapping reduced probability of parasitism for all three species, the probability of parasitism was higher for Black-capped Vireos compared to the other species in locations with and without cowbird trapping. Previous studies have also found relationships between parasitism frequency by Brown-headed Cowbirds and nest initiation date of hosts (Strausberger 1998, Ortega and Ortega 2000, Post van der Burg et al. 2009).

Woody cover and edge density, measured at two spatial scales around nests of Black-capped Vireos, were not associated with greater frequency of brood parasitism compared to the other two species. Previous research found that relationships between frequency of parasitism by Brown-headed Cowbirds and variables based on vegetation and landscape context depend on geographic location (Budnik et al. 2002, Tewksbury et al. 2006, Howell et al. 2007) and host species (Robinson et al. 1995, Burhans 1997, Woolfenden et al. 2003). Barber and Martin (1997) found that measurements of fine-scale nest site characteristics revealed no differences between nests of

Black-capped and White-eyed vireos, but vireo nests had less concealment and greater canopy cover than nests of Northern Cardinals; they found no differences in characteristics between parasitized and unparasitized nests for each species. It is also possible that parasitism frequency was associated with landscape variables at larger spatial scales than we included, as was found for songbirds nesting in woodlands (Robinson et al. 1995, Donovan et al. 1997). Such relationships may occur because cowbirds can commute up to 8 km between locations for feeding and parasitizing (Goguen and Mathews 2001, Kostecke et al. 2003).

Future studies could examine relationships between daily survival rate of nests and habitat metrics for Black-capped Vireos at larger spatial scales. Additionally, future research could address factors we were unable to evaluate, such as multiple brooding among the three species which is largely undocumented (Grzybowski 1995, Hopp et al. 1995, Halkin and Linville 1999), but which could influence population level responses to period nest survival. Similarly, population trajectory could vary among the three species because of variation in clutch size: White-eyed Vireos have a larger average clutch size of four (Hopp et al. 1995) compared to Black-capped Vireos, which average 3–4 (Grzybowski 1995), and Northern Cardinals which average 2–3 eggs per clutch (Halkin and Linville 1999).

Our inter-specific comparisons provided insight into why a species of conservation concern may have lower reproductive success than co-occurring species. Our results suggested cowbirds have more of an impact on Black-capped Vireos than Northern Cardinals and White-eyed Vireos where the species co-occur. Our study is unique because we provided nest success and brood parasitism estimates for the endangered Black-capped Vireo relative to two co-occurring species. Nest survival and brood parasitism estimates have limited meaning without comparative estimates, such as trends over time or across geographical locations, or, as in our case, co-occurring species. Furthermore, our study occurred on private properties, many of which did not have active habitat management practices for Black-capped Vireos. As demonstrated by our study, cowbird trapping alters local estimates of reproductive success, suggesting that studies conducted on properties that actively remove cowbirds do not adequately represent conditions occurring on unmanaged

lands. Our results suggest that cowbird removal, in addition to reducing parasitism, may be crucial for increasing period nest survival because it also reduces the nest predator effects of cowbirds.

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