



## Grazing Impact on Brood Parasitism in the Black-capped Vireo<sup>☆</sup>



Anthony J. Locatelli<sup>a,\*</sup>, Heather A. Mathewson<sup>b</sup>, Michael L. Morrison<sup>c</sup>

<sup>a</sup> Research Scientist, Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow, ID 83844, USA

<sup>b</sup> Assistant Professor, Department of Wildlife, Sustainability, and Ecosystem Sciences, Tarleton State University, TX 76402, USA

<sup>c</sup> Professor and Caesar Klaeberg Chair, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA

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### ABSTRACT

Grazing facilitates foraging opportunities for brown-headed cowbirds (*Molothrus ater*), an obligate brood parasite. Cowbirds can reduce productivity of their hosts, causing some host species to decline in abundance. Thus grazing indirectly influences productivity of some songbirds. The black-capped vireo (*Vireo atricapilla*) is an endangered songbird with most of its breeding range occurring in areas of ungulate grazing. A contributing factor to its endangered status is brown-headed cowbird parasitism. We monitored 382 black-capped vireo nests from 2012–2013 in Real, Kerr, Bandera, and Edwards Counties, Texas. We investigated how *enclosed ungulate* (characterized by the presence of enclosed ungulates) and *wild ungulate-only* (characterized by the absence of enclosed ungulates) systems influenced brood parasitism. We also examined how distance to water (distance from nest to nearest ungulate water source), nest concealment, and grassland in the landscape (proportion of grassland within 3 km of a nest) related to parasitism. Overall parasitism frequency was 30% ( $n = 166$ ) in 2012 and 31% ( $n = 216$ ) in 2013, moderate compared with other research, but above a proposed 30% threshold of concern. Grassland in the landscape was not important in predicting brood parasitism in wild ungulate-only grazing systems, but it was important in predicting brood parasitism in enclosed ungulate systems. In enclosed ungulate systems, there was low probability of brood parasitism with a small amount of grassland in the landscape and high probability of parasitism with a large amount of grassland in the landscape. Nest concealment and distance to water were not good predictors of brood parasitism.

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### Introduction

Anthropogenic land modification can have tremendous effects on biota through direct (e.g., habitat loss) and indirect (e.g., noise) impacts (Fischer and Lindenmayer, 2007). One widespread anthropogenic land modification is the change from free-roaming and native ungulate grazing and browsing systems to enclosed and exotic ungulate grazing and browsing systems. Grazing refers to consumption of herbaceous plants while browsing refers to consumption of nonherbaceous plants (Allen et al., 2011), but hereafter we refer to grazing and browsing collectively as *grazing*. Depending on the intensity, grazing can alter vegetation composition and structure (Kreuper et al., 2003; Gill and Fuller, 2007) and fauna composition, where some taxa may increase in abundance and others may decrease (Saab et al., 1995; Jones and Longland, 1999; Kreuper et al., 2003; Gill and Fuller, 2007; Burton et al., 2009).

One organism that can increase in local abundance as a result of livestock grazing is the brown-headed cowbird (*Molothrus ater*) (Young

and Hutto, 1999; Goguen and Mathews, 2000). Cowbirds forage on the ground, often in association with ungulates (Lowther, 1993), possibly because ungulates disturb invertebrate foods, making them more accessible, and because grazing may be associated with increased invertebrate densities (Morris and Thompson, 1998). Historically, cowbirds foraged with American bison (*Bison bison*; Mayfield, 1965; Ortega, 1998) and probably with other native ungulates. Currently, livestock are an important element of cowbird foraging habitat in many locations (Morris and Thompson, 1998). Cowbirds also forage in association with wild elk (*Cervus elaphus*; Goguen and Mathews, 2001), wild white-tailed deer (*Odocoileus virginianus*) in open landscapes (personal observation), and wild exotic ungulates in open landscapes (personal observation). Brown headed-cowbirds are obligate brood parasites that lay their eggs in nests of other species of birds and do not build their own nests and care for their own young (Robinson et al., 1995; Ortega, 1998). Cowbirds often remove host eggs (Robinson et al., 1995) and sometimes nestlings from the nest (Stake and Cavanagh, 2001; Conkling et al., 2012). When hosts are small in size, cowbird nestlings can out-compete host nestlings for provisions, leading to host nestling starvation and death (Lorenzana and Sealy, 1999). Cowbirds can reduce productivity of their hosts and have contributed to the decline of some endangered songbirds (Robinson et al., 1995; Rothstein and Peer, 2005).

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\* Correspondence: Anthony Locatelli, Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow, ID 83844, USA.

E-mail address: [loca0009@gmail.com](mailto:loca0009@gmail.com) (A.J. Locatelli).

<sup>1</sup> Current Address: Anthony Locatelli, 618 N. Adams St., Moscow, ID 83843, USA.

The black-capped vireo (*Vireo atricapilla*) is a migratory songbird with a current breeding range that includes parts of Oklahoma, Texas, and Mexico and formerly included a part of Kansas (Graber, 1961; Wilkins et al., 2006). Black-capped vireo habitat is generally shrubland, but they also inhabit deciduous and oak-juniper woodlands (Graber, 1961; Grzybowski et al., 1994; Pope et al., 2013). The black-capped vireo was listed as an endangered species in 1987 by the U.S. Fish & Wildlife Service because of habitat loss and cowbird parasitism (Wilkins et al., 2006).

Black-capped vireos are vulnerable to cowbird parasitism because they usually accept cowbird eggs (Farrell et al., 2010; Smith et al., 2012). Cowbird eggs hatch ~5 days before black-capped vireo eggs (Lowther, 1993; Grzybowski, 1995), and cowbirds are larger than black-capped vireos, which allow cowbird nestlings to outcompete vireo nestlings for food (Graber, 1961). Black-capped vireos almost never fledge from parasitized nests (Graber, 1961). Black-capped vireos also abandon parasitized nests at a high rate compared with unparasitized nests (Tazik, 1991). At the time of listing, black-capped vireos were frequently parasitized with an average parasitism rate of 80% across several study sites (Wilkins et al., 2006). More recent research reports the parasitism rate to range from 12% to 100% in different parts of the vireo range (Farrell et al., 2010; Pope, 2011; Smith et al., 2012). Cowbird control programs have had success in lowering parasitism (Wilkins et al., 2006), but control only takes place over a small portion of the black-capped vireo range.

Although grazing (browsing) can benefit black-capped vireos by retarding succession and maintaining vegetation in shrubland with a degree of openness (Grzybowski et al., 1994), grazing can also directly negatively affect black-capped vireos because nesting and foraging substrate is removed (Grzybowski, 1995). Whether grazing directly positively or negatively affects black-capped vireos probably depends on grazing intensity. Additionally, grazing facilitates foraging opportunities for cowbirds and therefore may indirectly affect vireo reproductive success.

Over 80% of the black-capped vireo breeding range is managed for livestock, and game ranching is also common in some parts of the vireo range (Wilkins et al., 2006). Much of the land can be described as either an *enclosed ungulate* system (enclosed and sometimes free-roaming ungulates) or a *wild ungulate-only* system (only free-roaming ungulates). We postulate that cowbirds are better able to predict enclosed ungulate locations than wild ungulate locations, so they will more often forage in enclosed ungulate systems (grazing system hypothesis). We predict enclosed ungulate systems will have higher nest parasitism than wild ungulate-only systems. In New Mexico, Goguen and Mathews (2000) found parasitism of plumbeous vireos (*Vireo plumbeus*) to be 81% in enclosed ungulate systems (referred to as *grazed*) and approximately 60% in wild ungulate-only systems (referred to as *ungrazed*). Goguen and Mathews (2001) found that 98% of cowbird foraging observations were in association with enclosed cattle or horses rather than with wild elk; cowbirds that bred in wild ungulate-only systems almost exclusively commuted to enclosed ungulate systems to forage with enclosed cattle and horses rather than forage with wild elk present in wild ungulate-only systems.

Grassland in the landscape (area within 3 km of a nest) may also influence parasitism because grassland is preferred cowbird foraging habitat (Thompson, 1994; Morris and Thompson, 1998) and cowbirds regularly commute between foraging and breeding areas (Rothstein et al., 1984; Thompson, 1994; Curson et al., 2000). Telemetry studies indicate the average commute is 1–3 km (Thompson, 1994; Gates and Evans, 1998; Goguen and Mathews, 2001; Kostecke et al., 2003), though individual cowbirds regularly commute 15 km (Curson et al., 2000). A nearby cowbird foraging area may have affected the parasitism rate in Kentucky warblers (*Oporornis formosus*) where 60% of nests within 300 m of the cowbird foraging area were parasitized, while only 3% of nests > 1500 m were parasitized (Morse and Robinson, 1999). We postulate cowbirds forage more often in areas with a large proportion of grassland in the landscape relative to areas with a small proportion of grassland in the landscape because of the corresponding difference in

amount of cowbird foraging habitat (grassland in the landscape hypothesis). We predict nests with a large proportion of grassland in the surrounding landscape (within 3 km) will be parasitized frequently relative to nests with a small proportion of grassland in the landscape.

Distance to ungulate water source is another factor that could be related to brood parasitism. Horses (Girard et al., 2013), cattle (Kaufmann et al., 2013), and female white-tailed deer (Brunjes et al., 2006) prefer habitat close to water. We postulate ungulates graze areas close to water more than areas far from water because they need to return to water regularly to hydrate, and therefore cowbirds forage more often near ungulate water sources (distance to water hypothesis). We predict nests closer to ungulate water sources will be parasitized more frequently than nests farther from ungulate water sources. Our hypothesis and prediction are supported by Coker and Capen (1995), who found that cowbirds were most abundant in areas where the concentration of livestock grazing areas was greatest, and Kostecke et al. (2003), who found that a reduction in stocking rate from 752 to 103 animal units (0.08–0.01 animal units per ha) was associated with reduced parasitism.

Though grazing-related factors may have a large effect on parasitism, nest concealment could also be influential. The nest concealment hypothesis (also termed the *nest exposure hypothesis*) states cowbirds have difficulty detecting well-concealed nests and more easily detect exposed nests (Hauber and Russo, 2000; Saunders et al., 2003; Fiorini et al., 2012). We predict well-concealed nests will be parasitized less frequently than more concealed nests. Some studies indicate nest concealment influences cowbird parasitism of songbirds (Burhans, 1997; Saunders et al., 2003; Sharp and Kus, 2006) whereas others do not (Hauber and Russo, 2000; Ortega and Ortega, 2001). In a study of black-capped vireos, Barber and Martin (1997) did not find nest concealment to be an important factor contributing to parasitism.

Our objectives were to 1) describe cowbird parasitism frequency in black-capped vireos in areas without cowbird control to further assess its status and 2) assess how the following factors relate to cowbird parasitism of black-capped vireos: grazing system, grassland in the landscape, distance to water, and nest concealment.

## Methods

### Study Area

We conducted our research in 2012 and 2013 on public and private lands in Real, Bandera, Kerr, and Edwards counties, Texas. Our study sites were located in the Edwards Plateau ecoregion and within the black-capped vireo recovery region 2 (Wilkins et al., 2006). Proportion of pastureland, which the US Department of Agriculture defines as primarily grazing land, ranges from approximately 60% to 80% in each county of our study area (NASS, 2007). Free-roaming white-tailed deer, axis deer (*Axis axis*), aoudad (*Ammotragus lervia*), and wild hogs (*Sus scrofa*) are common (personal observation); we are not aware of any recent population estimates of these mostly exotic species specific to our study area. Despite landowners' best efforts, many free-roaming exotic populations are the result of escaped ungulates. Private landowners use high fencing (not passable by any ungulate), traditional low fencing (passable by some ungulates but not others), or land features (i.e., a cliff) to enclose their ungulates. These enclosures divide the land into either 1) *enclosed ungulate* systems: enclosed livestock (cattle, goats, horses); American bison; and/or exotic ungulates and sometimes wild ungulates present (white-tailed deer, axis deer, aoudad, feral hogs) or 2) *wild ungulate-only* systems: no enclosed ungulates, only wild, free-roaming ungulates present (white-tailed deer, axis deer, aoudad, feral hogs).

Our study area is composed of a mixture of shrubland, grassland, and oak/juniper woodland. Major plant species include live oak (*Quercus virginiana*), Ashe juniper (*Juniperus ashei*), Texas oak (*Quercus buckleyi*), shin oak (*Quercus sinuata*), mountain laurel (*Sophora secundiflora*), Texas persimmon (*Diospyros texana*), little bluestem (*Schizachyrium*

scoparium), Texas grama (*Bouteloua rigidisetata*), and prickly pear (*Opuntia* spp.). In 2012 and 2013, precipitation and temperature were similar to long-term averages during the black-capped vireo breeding season (March to July); average monthly precipitation is approximately 6.6 cm and average monthly temperature is approximately 22.2°C (NOAA, 2014).

#### Site Selection

McFarland et al. (2013) randomly surveyed properties in our study area and detected black-capped vireos at some properties. We also knew of one additional property with prior vireo detections. We requested access to all properties where vireos had been detected previously, but we were not granted access to a sufficient amount of properties to reach our goal of 6–7 study sites per year. To select additional properties, we randomly selected a property owner name and then visually scanned aerial imagery of the property for potential black-capped vireo habitat. Each accessible property with prior vireo detections or unsurveyed property with potential vireo habitat became a potential site. At each potential site, we surveyed for black-capped vireos by listening and watching for them while systematically walking transects 200 m apart, placed in potential habitat. We determined the length of each transect by the extent of potential habitat. We surveyed each potential site two to three times between 25 March and 21 April in 2012 and 2013. We conducted surveys between sunrise and 5 hours after sunrise. If we did not detect a vireo, we did not select the potential site for study and surveyed alternative potential sites. If we detected at least one vireo and it remained territorial, we selected the potential site for study. Levels of parasitism had never been measured at any of the study sites we selected.

The mean nearest distance between study sites was 28.3 km, and the distance between sites ranged from 1.5 to 67.8 km. The size of our sites ranged from 93 to 564 ha with a mean size of 186 ha. We had seven sites in 2012 and six sites in 2013. We eliminated one 2012 site from the analysis because there was a brown-headed cowbird trap 930 m from the nearest nest, and this potentially affected parasitism frequency. In the 12 remaining sites, there were no cowbirds trapped within 2 km of a nest in the year we collected data. Six sites were in enclosed ungulate systems and six sites were in wild ungulate-only systems. The six enclosed ungulate system sites were continuously grazed during our periods of data collection. Of the six enclosed ungulate system sites, two enclosed cattle only, one enclosed cattle and exotic ungulates, one enclosed bison and exotic ungulates, one enclosed horses and exotic ungulates, and the last enclosed only exotic ungulates.

#### Nest Searching and Monitoring

At each site we mapped black-capped vireo territories by following males at a distance of 20 m and marking global positioning system (GPS) points. We visited each territory for a maximum of 60 minutes per day every 2–10 days between sunrise and 7 hours after sunrise. If there were more than 24 territories at a site, we randomly chose a subset of 24 territories to monitor. We located nests through behavioral observations and by vegetation searching. After we located a nest, we monitored it every 2–4 days until the nest was no longer active. We used direct observation, a nest mirror, or binoculars to determine the contents of the nest. We only considered nests observed with contents (at least one egg or nestling) for analysis. We considered a nest parasitized if at least one brown-headed cowbird egg or nestling was in the nest and unparasitized if all contents were black-capped vireo. If the timing was appropriate for fledglings and nestlings were not in the nest, we searched the territory for fledglings and adults. We determined nests to be successful if we observed a fledgling, adult carrying food, fledgling begging calls, or an adult was extremely defensive (bill snapping, extreme straddling) near the nest. After a nest was no longer active, we documented the location of the nest using a GPS unit.

#### Grassland in the Landscape

Because the average commute of a cowbird typically ranges between 1 and 3 km (Thompson, 1994; Gates and Evans, 1998; Goguen and Mathews, 2001; Kostecke et al., 2003), we chose a 3-km radius circle around each nest to represent the surrounding landscape. We assume that these landscapes encompass most foraging areas of most cowbirds breeding in the area but recognize that some individual cowbirds may commute longer distances (Curson et al., 2000). We acquired the 2012 National Agriculture Imagery Program 1-m spatial resolution aerial photos of the area. The imagery was collected during the 2012 growing season using a Cessna 441 aircraft, which carried a Leica Geosystem's ADS80/SH82 digital sensor that recorded in four bands: blue (420–492 nm), green (533–587 nm), red (604–664 nm), and near infrared (833–920 nm). In ENVI 5.0 (Exelis Visual Information Solutions, 2013) using the supervised maximum likelihood method, we classified the imagery into four landcover classes: grassland, woody (trees and shrubs), water, and bare (pavement, gravel roads, unvegetated areas). We assessed the accuracy of our classification by comparing 256 reference points to the classified image. We established the reference points by randomly placing the points over the classified image and then assigning each point a true class by interpreting Google Earth imagery; each class had at least 30 reference points. To calculate the proportion of grassland in the landscape around each nest, we divided the area of grassland by the total area of the 3-km circle.

#### Distance to Water

Ungulate water sources were any type of water that remained for the entire breeding season, including water troughs, ponds, or rivers. Using a GPS unit, we recorded locations of water that landowners informed us of and any water encountered during the course of fieldwork. After confirming correct classification through visual interpretation of the imagery, we used our classified image to create polygons of areas covered by water. Because our classified image was 84.4% accurate (see results), we also visually scanned the aerial imagery for any water that was not accounted for using the preceding methods. We combined all of this information to form a single polygon layer in ArcGIS 10.0 (ESRI, 2010) and used ArcGIS 10.0 (ESRI, 2010) to calculate distances from nests to nearest water sources.

#### Nest Concealment

We considered five variables potentially representative of the nest concealment hypothesis: nest height (Nest\_height), distance from the nest to nearest edge of woody vegetation (Dist\_edge), and maximum diameter of the woody vegetation clump where the nest was located (Max\_diameter). We measured visual obstruction of the nest (Vis\_obstruction), which was the average of six estimates of the percent of the nest blocked from view. The observer visually estimated the percent of each nest blocked from view to the nearest 10%. We took the estimates at 1-m distance from the nest in each cardinal direction, above and below the nest. If estimating from this distance and perspective was not possible, we took the estimate from the nearest possible vantage point. We also considered 5) cover (Cover), which was the average of 80 estimates of percent of a 0.1 m × 0.1 m section of a cover-board blocked from view. The cover-board was a 2 m × 0.1 m board divided into 20 sections (0.1-m intervals). We placed the cover-board directly in front of the nest and took the estimates at 7-m distance in each cardinal direction. Cowbirds typically perch atop trees and shrubs to search for adults visiting nests, so higher nests would be closer to a perching cowbird with less vegetation in between and presumably less concealed. We also predicted nests closer to the edge of woody vegetation, and nests within vegetation clumps with a smaller maximum diameter would be less concealed and parasitized more often because they would have less vegetation between the nest and a perching

cowbird. We predicted that nests with more visual obstruction and more cover would be more concealed and parasitized less often because cowbirds would have a more difficult time seeing adults visiting nests and detecting a nest.

*First Egg Ordinal Date*

In black-capped vireos, parasitism probability increases as the breeding season progresses with a slight decline at the end of the breeding season (Campomizzi et al., 2013). To control for time of nest initiation in our modeling approach (see analysis), we estimated the first egg ordinal date by interpreting nest check data and backdating, assuming one egg was laid per day. Black-capped vireos have an incubation period of 14–17 days and a nestling period of 10–12 days (Grzybowski, 1995). Therefore we used a 15-day incubation period and an 11-day nestling period to backdate. If the nest was parasitized and nestlings present, we used an 11-day incubation period and 10-day nestling period to backdate because brown-headed cowbird incubation period is 10–12 days and their nestling period is 8–13 days (Lowther, 1993). If nest check data revealed variation to these period lengths for individual nests, we refined the first egg ordinal date estimate accordingly. If we found an active nest with a full clutch, but it failed before we observed hatching, we backdated to the first egg ordinal date by subtracting the median amount of possible days since the first egg was laid from the date the nest was first observed.

*Data Analysis*

We used a  $\chi^2$  test to compare proportion of abandoned parasitized nests against abandoned unparasitized nests and predated parasitized nests against predated unparasitized nests. We used an information-theoretic approach (Aikaike’s Information Criterion adjusted for small sample sizes [AIC<sub>c</sub>]; Anderson, 2008) to assess relative influence of grazing system, grassland in the landscape, distance to water, and nest concealment on parasitism. We used R statistical software 3.0.2 (R core team, 2013) to create logistic regression models using the link logit function with a binary response variable, parasitized or unparasitized. We examined residuals for nonlinear trends and found they were not important. To control for timing of nest initiation, we included the ordinal date of the first egg laid as a predictor variable for all models. We evaluated evidence of multicollinearity using variance inflation factors (VIFs) of the global model, considering VIFs > 10 to be evidence of multicollinearity (Ott and Longnecker, 2010) and used a Hosmer–Lemeshow goodness-of-fit test to assess goodness of fit of the global model (Hosmer and Lemeshow, 2000).

We considered four hypotheses to predict parasitism: the grazing system hypothesis, the grassland in the landscape hypothesis, the distance to water hypothesis, and the nest concealment hypothesis. We represented each grazing-related hypothesis with one predictor variable and the nest concealment hypothesis with five predictor variables (Table 1). Because we had five predictor variables representing the nest concealment hypothesis, we first determined competitive models for that hypothesis because we sought to represent each respective hypothesis only with models that were competitive for the best model. We divided our model evaluation into two stages with the first focusing on the nest concealment hypothesis and the second stage focusing on all hypotheses.

For the first nest concealment hypothesis evaluation stage, we ran five models, each with one respective nest concealment hypothesis predictor variable and ordinal date of the first egg laid. We also ran a null model with only the ordinal date of the first egg laid included. If a model ranked above the null and within 2  $\Delta$ AIC<sub>c</sub> of the best model, we included that model in stage 2 of our model evaluation to represent the nest concealment hypothesis.

We evaluated all four hypotheses in the second stage of our model evaluation. We constructed 11 models from our four a priori hypotheses

about factors that potentially influence parasitism. We included additive terms for each of the grazing hypotheses variables and the nest concealment hypothesis variable that met our criteria for inclusion. In one model, we included an interaction term of grazing system and grassland in the landscape to assess whether the influence of grassland in the landscape depended on the grazing system. We also included models with an interaction term of the nest concealment variable and each grazing variable to assess if the influence of nest concealment depended on any grazing variable. We also included a model with an interaction term of grazing system and distance to water to assess if the presence of enclosed ungulates is a prerequisite for distance to water to be influential. We considered models with  $\Delta$ AIC<sub>c</sub> < 2 to have substantial support for being the best model (Burnham and Anderson, 2002) and models with  $\Delta$ AIC<sub>c</sub> 2–4 and fewer parameters than the top-ranked model to have some support as a plausible model. Using all models, we report model-averaged coefficient estimates and 95% unconditional confidence intervals (Anderson, 2008), which we used to evaluate variables. We used the plausible models to predict probability of parasitism.

**Results**

*Description*

We located 166 nests from 100 territories in 2012 and 216 nests from 104 territories in 2013 for a total of 382 nests. We found 65% of nests early in the nesting sequence (building, laying, or within 4 days of the onset of incubation). The earliest first egg dates were 3 April in 2012 and 7 April in 2013. The latest first egg dates were 27 June in 2012 and 5 July in 2013. The overall parasitism rate was 31% ( $n = 382$ ; 2012: 30%,  $n = 166$ , 2013: 31%,  $n = 216$ ). We observed 9% (2012: 6%,  $n = 50$ , 2013: 12%,  $n = 68$ ) of parasitized nests to contain two cowbird eggs or nestlings. We did not observe any parasitized nests with > two cowbird eggs. Adult vireos abandoned fewer unparasitized nests (4%,  $n = 264$ ) than parasitized nests (29%,  $n = 118$ ;  $\chi^2 = 45.33$ ,  $df = 1$ ,  $P < 0.001$ ). Apparent nest success was 30% ( $n = 166$ ) in 2012 and 27% ( $n = 216$ ) in 2013. Mayfield estimates of daily survival rate for incubation and nestling periods combined were  $0.967 \pm 0.003$  SE in 2012 and  $0.962 \pm 0.003$  SE in 2013. Over both years, 6 of 118 parasitized nests (5%) fledged  $\geq 1$  black-capped vireo young. In these cases, the brown-headed cowbird egg either never hatched ( $n = 4$ ) or the cowbird egg or nestling was likely predated while vireo young survived ( $n = 2$ ). Excluding abandoned nests, 53%

**Table 1**

Variables included in logistic regression models predicting probability of cowbird parasitism of black-capped vireo nests in Texas, 2012–2013. Variables form part of four hypotheses; time of nest initiation (Ordinal\_date) was included in all models

Variable	Definition (units)
<b>A Nest Concealment Hypothesis</b>	
Nest_height	Height of nest, measured from the ground to nest rim (m)
Dist_edge	Distance from nest to nearest edge of woody vegetation clump (m)
Vis_obstruction	Average of 6 estimates of percent of nest visually obstructed (%)
Max_diameter	Maximum diameter of woody vegetation clump (m)
Cover	Average of 80 estimates of percent cover-board section visually obstructed (%)
<b>B Grazing Hypotheses</b>	
Dist_water	Distance from nest to the nearest ungulate water source (m)
Grassland_landscape	Grassland in the landscape, proportion grassland within 3 km of nest (%)
System	Enclosed ungulate or wild ungulate–only grazing system
<b>C Temporal</b>	
Ordinal_date	Time of nest initiation, ordinal first egg date (days)

**Table 2**

Selection of logistic regression models predicting brown-headed cowbird parasitism of black-capped vireo nests for the **A**, nest concealment hypothesis and **B**, grazing system, grassland in the landscape, distance to water, and nest concealment hypotheses for nests monitored in Texas, 2012–2013. Nest\_height was the height of the nest, measured from the ground to the nest rim. Dist\_edge was the distance from the nest to the nearest edge of the woody vegetation clump. Vis\_obstruction was the average of 6 estimates of the percent of the nest visually obstructed. Max\_diameter was the maximum diameter of the woody vegetation clump that the nest was in. Cover was the average of 80 estimates of the percent of a cover-board section visually obstructed. Dist\_water was the distance from the nest to the nearest ungulate water source. Grassland\_landscape was the proportion of grassland within 3 km of a nest. System was a categorical variable classified as either an enclosed grazing system or wild ungulate-only grazing system

Model <sup>1</sup>	K <sup>2</sup>	$\Delta AIC_c$ <sup>3</sup>	W <sub>i</sub> <sup>4</sup>	LL <sup>5</sup>
<b>A Nest Concealment Hypothesis Models</b>				
Nest_height	3	0.00	0.44	-203.93
Null	2	2.07	0.16	-205.98
Vis_obstruction	3	2.09	0.16	-204.97
Cover	3	2.42	0.13	-205.14
Dist_edge	3	3.95	0.06	-205.91
Max_diameter	3	4.11	0.06	-205.98
<b>B Multihypothesis Models</b>				
System * Grassland_landscape	5	0.00	0.59	-192.36
Grassland_landscape	3	2.32	0.19	-195.57
Grassland_landscape * Nest_height	5	2.87	0.14	-193.79
System + Grassland_landscape	4	4.31	0.07	-195.54
System * Nest_height	5	9.18	0.01	-196.95
Dist_water * Nest_height	5	12.08	0.00	-198.40
System	3	12.74	0.00	-200.78
System * Dist_water	5	15.74	0.00	-200.23
Nest_height	3	19.04	0.00	-203.93
Null	2	21.12	0.00	-205.98
Dist_water	3	21.88	0.00	-205.35

<sup>1</sup> All models include a time of nest initiation variable. Models with an interaction term (with “\*”) include additive terms for each variable.

<sup>2</sup> Number of parameters.

<sup>3</sup> Difference between Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ) value of current model and most-supported model.

<sup>4</sup>  $AIC_c$  weight or relative likelihood the model is the best model.

<sup>5</sup> Log likelihood value.

( $n = 253$ ) of unparasitized nests were predated while 63% ( $n = 84$ ) of parasitized nests were predated ( $\chi^2 = 2.04$ ,  $df = 1$ ,  $P = 0.153$ ). Overall accuracy of the landcover classification was 84.4%.

### Model Selection

We could not estimate ordinal first egg date for 18 nests, so we reduced the dataset to 364 nests for model evaluation. The global model did not show evidence of lack of fit (Hosmer–Lemeshow goodness-of-fit:  $\chi^2 = 10.65$ ,  $P = 0.22$ ) or evidence of multicollinearity among predictor variables ( $VIFs < 3$ ). For the nest concealment hypothesis model evaluation (first stage), only the nest height model ranked above the null (Table 2) and was the only variable we used in construction of multihypothesis models. In our multihypothesis model evaluation (second stage), the model including an interaction term for system and grassland in the landscape (see Table 2) was the best fit model and the only model to receive substantial support as the best model ( $\Delta AIC_c < 2$ ). Another model including an additive term for grassland in the landscape (see Table 2) received some support as a plausible model ( $\Delta AIC_c = 2.32$ ). Both models had unconditional 95% confidence intervals that did not include 0 (Table 3). In wild ungulate-only systems, the best fit model predicted relatively low probability of parasitism with similar predicted probability across different amounts of grassland in the landscape (Fig. 1). In enclosed ungulate systems, the best fit model predicted relatively low probability of parasitism when the amount of grassland in the landscape was relatively low and it predicted relatively high probability of parasitism when the amount of grassland in the landscape was high (see Fig. 1). The other plausible model including an additive term for grassland in the landscape predicted relatively low probability of parasitism when the amount of

**Table 3**

Model-averaged coefficients and 95% unconditional confidence intervals from models predicting cowbird parasitism of black-capped vireo nests from Texas, 2012–2013. Nest\_height was the height of the nest, measured from the ground to the nest rim. Dist\_edge was the distance from the nest to the nearest edge of the woody vegetation clump. Vis\_obstruction was the average of 6 estimates of the percent of the nest visually obstructed. Max\_diameter was the maximum diameter of the woody vegetation clump that the nest was in. Cover was the average of 80 estimates of the percent of a cover-board section visually obstructed. Dist\_water was the distance from the nest to the nearest ungulate water source. Grassland\_landscape was the proportion of grassland within 3 km of a nest. System was a categorical variable classified as either an enclosed grazing system or wild ungulate-only grazing system. Ordinal\_date was the ordinal first egg date

Variable	B <sup>1</sup>	CI <sup>2</sup>
Nest_height	0.3739	0.0106, 0.7373
Dist_water	0.0003	-0.0003, 0.0009
Grassland_landscape	3.6670	1.7939, 5.5402
System	0.0758	-0.6890, 0.8406
System * Grassland_landscape	-6.7872	-12.0509, -1.5235
Grassland_landscape * Nest_height	2.3352	-0.5034, 5.1739
System * Nest_height	-0.9980	-1.8630, -0.1329
Dist_water * Nest_height	0.0017	0.0005, 0.0029
System * Dist_water	-0.0002	-0.0014, 0.0010
Ordinal_date	0.0236	0.0128, 0.0344

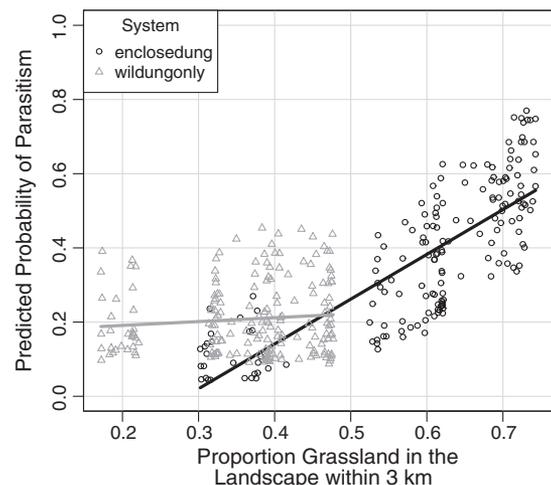
<sup>1</sup> Model-averaged coefficient.

<sup>2</sup> 95% unconditional confidence interval.

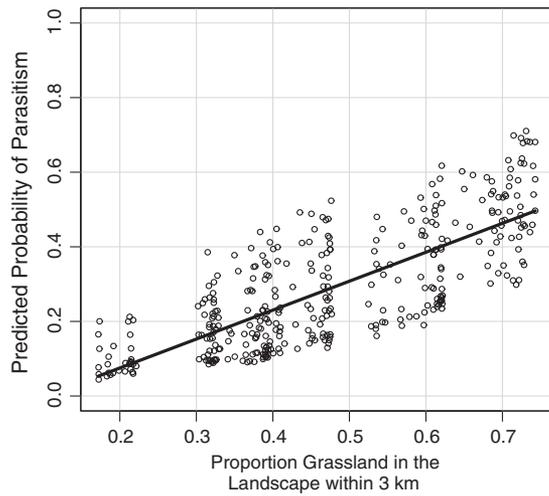
grassland in the landscape was relatively low, and it predicted relatively high probability of parasitism when the amount of grassland in the landscape was high (Fig. 2).

### Discussion

The amount of grassland within 3 km did not influence probability of parasitism in wild ungulate-only systems, but in enclosed ungulate systems the probability of parasitism increased as the amount of grassland within 3 km increased. Cowbirds should prefer the closest available breeding areas to their foraging areas because shorter commutes allow for more energy to be expended on foraging and egg production (Curson and Mathews, 2003). Enclosed ungulate systems may provide a reliable source of ungulates, and the amount of grassland in the landscape may reflect the number and distribution of cowbird foraging opportunities. Enclosed ungulate systems with a high proportion of grassland in the landscape may have a higher number of, and likely more distributed, cowbird foraging opportunities leading to higher



**Fig. 1.** Predicted probability of cowbird parasitism of black-capped vireo nests plotted against the proportion of grassland in the landscape within 3 km of nests for enclosed ungulate systems (enclosedung) and wild ungulate only systems (wildungonly). We used the best fit logistic regression model to predict probability of parasitism of a nest, based on nests monitored in Texas, 2012–2013.



**Fig. 2.** Predicted probability of cowbird parasitism of black-capped vireo nests plotted against the proportion of grassland in the landscape within 3 km of nests. We used the second best logistic regression model to predict probability of parasitism of a nest, based on nests monitored in Texas, 2012–2013.

probability of parasitism because cowbirds more often have a relatively short commute. Wild ungulate-only systems may have a relatively low probability of parasitism regardless of grassland in the landscape because a reliable source of ungulates and foraging opportunities have to be found elsewhere, meaning cowbirds breeding in wild ungulate-only systems have to commute farther distances. The increased commute may lead to lower cowbird abundance and lower egg production per cowbird. The availability and distribution of cowbird foraging opportunities likely were the underlying mechanisms that influenced parasitism in our study.

Our results are consistent with research that suggests a relationship between cowbird foraging opportunities and parasitism in other passerines (Pietz et al., 2009; Falk et al., 2011; Cox et al., 2012; Hovick and Miller, 2013) but contrasts other research (Benson et al., 2010). Falk et al. (2011) examined grassland and row crop in the landscape (cowbird foraging areas) association with parasitism and found a positive correlation with both. Pietz et al. (2009), Cox et al. (2012), and Hovick and Miller (2013) examined woodland in the landscape (not cowbird foraging areas) association with parasitism and found a negative correlation, showing a lack of foraging opportunities is associated with reduced parasitism. Campomizzi et al. (2013) did not find evidence of a relationship between black-capped vireo nest parasitism and woody cover within 500 m of each nest, essentially the inverse of our grassland in the landscape variable. They suggested they may not have found a link because they did not include a large enough area around each nest to account for cowbirds commuting long distances. Our results support their speculation because we included the area within 3 km of a nest rather than 500 m. Campomizzi et al. (2013) also may not have found a link between woody cover and parasitism because they compared woody cover with nest initiation date, and nest initiation date may have had a large effect relative to woody cover. We also found an influence of time of nest initiation on parasitism; nests were more likely to be parasitized as the breeding season progressed. Campomizzi et al. (2013) found a similar pattern; nests were more likely to be parasitized as the breeding season progressed, though they found a slight decline in parasitism probability at the very end of the breeding season, which we did not. In the beginning of the season, more birds are initiating nests and the large number of nests may dilute parasitism frequencies. As the season progresses, fewer nests are available for the same number of cowbirds, so nests may be parasitized more frequently.

Our results indicate enclosed systems influence parasitism, possibly because enclosures limit ungulate movement and provide more

predictable cowbird foraging opportunities. Yet another factor we were unable to assess was ungulate type. Using telemetry, Goguen and Mathews (2001) and Goguen et al. (2005) found cowbirds prefer to forage with cattle, bison, or horses over elk and pronghorn antelope (*Antilocapra americana*). Cowbird ungulate-type preference may depend on ungulate vegetation-type use. For example, white-tailed deer spend much of their time in nongrassland areas because they are browsers (Deperno et al., 2002), feeding on nonherbaceous plants. Cattle and horses are grazers and spend more time in grassland (Lamoot et al., 2005), cowbirds' main foraging vegetation (Morris and Thompson, 1998). Movement patterns, including how fast an ungulate moves while grazing, could also influence efficiency of cowbird foraging. Time of grazing activity may have an influence as cowbirds tend to breed in the morning and forage in the afternoon (Goguen and Mathews, 2001); cowbirds may prefer ungulates that actively graze during the afternoon. Ungulates that congregate in large herds may provide more foraging opportunities than ungulates that spend most of their time solitary or in small herds. It is possible some or all of these ungulate characteristics combine to determine cowbird ungulate-type preference. Future research could further examine the influence of ungulate type on cowbird foraging and parasitism.

We did not observe an influence of distance to water on parasitism. We used distance to water to serve as a proxy of grazing intensity because some ungulates prefer to be near water (Brunjes et al., 2006; Girard et al., 2013; Kaufmann et al., 2013), so we assumed they would graze more often there. We acknowledge our assumption could or could not be true and that a direct measure of grazing intensity such as stocking rate may have produced different results. We could not consider stocking rate because it was not available for wild ungulate-only systems and landowners sometimes did not know how many ungulates they had in enclosed ungulate systems. This was especially true for sites that had exotic ungulates because exotic ungulates were often left to breed freely and unknowingly to the landowner. We also acknowledge a potential relationship between distance to water and nest parasitism could be explained by cowbirds' need for water, but we consider this explanation less likely than grazing intensity because cowbirds can acquire water through their diet and other natural sources (e.g., dew and rain puddles). Kostecke et al. (2003) measured stocking rate and found that parasitism in black-capped vireos decreased by decreasing stocking rate. At a consistently grazed site, Kostecke et al. (2003) observed a reduction in stocking rate (0.08–0.01 animal units per ha) and compared parasitism in the prereluction time period with parasitism in the postreluction time period; parasitism decreased sharply (19–35% to 2–3%). Our inconsistent results with Kostecke et al. (2003) suggest distance to water may not be a good proxy of grazing intensity. Perhaps we did not observe an effect because approximately 75% of nests were within 1 km of water, which could be too small of variation in distance to influence ungulate and cowbird movements and behavior.

Our results did not indicate an important effect of nest concealment because models with nest concealment variables received little support. Nest concealment may not influence parasitism because cowbirds' primary nest searching strategy may be by observing host behavior and not by vegetation searching (Robinson and Robinson, 2001). For example, cowbirds may detect nests by observing adults bringing nest material to a consistent location (Robinson and Robinson, 2001). There is ample opportunity as hosts make hundreds of trips with nesting material. Our results are consistent with Barber and Martin (1997), who did not find any difference in nest characteristics between parasitized and unparasitized black-capped vireo nests.

The overall level of parasitism we observed was slightly above the  $\geq 30\%$  threshold of concern for black-capped vireos (Smith et al., 2013). It is important to note that cowbird parasitism rates can fluctuate substantially (Wilkins et al., 2006), and we only observed parasitism in 1 year per site. We observed low overall parasitism frequencies compared with Farrell et al. (2010; 100%,  $n = 20$ ) and comparable parasitism with Smith et al. (2012; 34%,  $n = 119$ ), where both studied other

parts of the vireo range without cowbird control efforts. Our observed parasitism rate was substantially lower than the 80% rate observed across several areas before the initiation of cowbird control in Texas in 1988 (Wilkins et al., 2006). From 1985 to 1988, parasitism at one site in Kerr County ranged from 65% ( $n = 20$ ) to 90% ( $n = 10$ ) (Wilkins et al., 2006). The moderate parasitism we observed in Kerr and surrounding counties could be partly due to a cowbird population decline in the Edward's Plateau from 1966 to 2011 (Sauer et al., 2012).

## Implications

To enhance breeding habitat for black-capped vireos, we suggest land managers focus cowbird trapping and euthanasia in enclosed ungulate systems with a large amount of grassland in the landscape. If an entity seeks to protect land for the benefit of black-capped vireos, we suggest targeting wild ungulate-only systems or enclosed ungulate systems with a small amount of grassland in the landscape. To lower brood parasitism of black-capped vireos, land managers could remove enclosed ungulates from black-capped vireo breeding areas during the vireo breeding season, making them wild ungulate-only systems during that period. Managing vireo breeding areas as enclosed ungulate systems during the vireo nonbreeding season could potentially be compatible with black-capped vireo conservation because individual cowbirds that would potentially be attracted to and winter in these areas would likely migrate before black-capped vireos began breeding.

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