GRAZING IMPACT ON BROOD PARASITISM

A Thesis

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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May 2014

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Anthropogenic land use changes can have tremendous direct and indirect effects
on biota. A prevalent land use change in Texas is conversion of land to grazing.
Grazing facilitates foraging opportunities for brown-headed cowbirds (*Molothrus ater*),
a 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 livestock and other ungulate
grazing. A contributing factor to its endangered status is brown-headed cowbird
parasitism. I monitored 382 black-capped vireo nests from 2012-2013 in Real, Kerr,
Bandera and Edwards counties, Texas and described parasitism. I investigated how
grazing system related to parasitism; I defined grazed systems by the presence of
enclosed ungulates and wild ungulate only systems by the absence of enclosed
ungulates. I also examined how grazing intensity (represented by distance from nest to
nearest ungulate water source), nest concealment, and grazing in the landscape
(represented by proportion of grassland within 3 km of a nest), related to parasitism.
Overall parasitism was 30% ($n = 166$) in 2012 and 31% ($n = 216$) in 2013, moderate
compared to other research, but above a proposed threshold of concern. Grazing system
and grazing in the landscape interacted in predicting probability of parasitism. Grazing
in the landscape was not important in predicting brood parasitism in wild ungulate only
grazing systems, but was important in predicting brood parasitism in grazed systems. In

grazed systems, there was low probability of brood parasitism with low grazing in the landscape and high probability of parasitism with high grazing in the landscape. Nest concealment and grazing intensity were not good predictors of brood parasitism. Land managers could use this information to prioritize cowbird management or preservation efforts.

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INTRODUCTION

Anthropogenic land use changes 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 change is conversion of land to ungulate

grazing and browsing. Grazing refers to consumption of herbaceous plants while

browsing refers to consumption of non-herbaceous plants (Allen et al. 2011), but

hereafter I refer to grazing and browsing collectively as grazing. Texas leads the nation

in sheep, goat, and cattle production and has approximately 247,500 farms and ranches

encompassing 52.8 million ha (Staples 2006).

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, Gill and Fuller

2007, Burton et al. 2009). Grazing can be a useful tool for managing exotic plants and

in conservation efforts of some songbirds (Johnson and Sandercock 2010). Grazing can

also reduce foraging and nesting habitat of birds (Gill and Fuller 2007). Further, high

grazing intensity can reduce seasonal fecundity in songbirds (Pedersen et al. 2007). In

Texas, over-grazing is a problem for some birds (Wilkins et al. 2006).

One species that has increased its continental range and abundance as a result of

land conversion to livestock grazing is the brown-headed cowbird (*Molothrus ater*)

(Mayfield 1965, Robinson et al. 1995). Brown-headed cowbirds feed on the ground,

often in association with ungulates (Lowther 1993), possibly because ungulates increase

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their food availability (Morris and Thompson 1998). Historically, cowbirds foraged with American bison (*Bison bison*; Friedman 1929, Mayfield 1965) and probably with other native ungulates. Currently, livestock are an important element of cowbird foraging habitat in many locations (Morris and Thompson 1998). Cowbirds forage in association with elk (*Cervis elaphus*; Goguen and Mathews 2001), white-tailed deer (*Odocoileus virginianus*), and exotic ungulates (personal observation).

Brown headed-cowbirds are brood parasites; brood parasites lay their eggs in nests of other species of birds (Friedman 1929, Robinson et al. 1995). Cowbirds often remove host eggs (Robinson et al. 1995) and nestlings from the nest (Stake and Cavanagh 2001). In addition, cowbird nestlings often hatch sooner, are larger, grow faster, and beg more loudly than some host nestlings, which stimulates the adult host to feed them more often (Robinson et al. 1995). Small host nestlings are often outcompeted by the nestling cowbirds for food and small hosts often fail to fledge any of their own young (Robinson et al. 1995). Because cowbirds can reduce productivity of their hosts, they have contributed to the decline of endangered songbirds (Robinson et al. 1995, Rothstein and Peer 2005).

The black-capped vireo (*Vireo atricapilla*) is a migratory songbird with a current known breeding range that includes parts of Oklahoma, Texas, and Mexico and formerly included parts of Kansas (Graber 1961, Wilkins et al. 2006). Black-capped vireo habitat generally consists of low, patchy, and woody vegetation, 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 vegetation succession, habitat loss caused by land use conversion, browsing and grazing by wild and domestic herbivores, and brown-headed cowbird parasitism (Ratzlaff 1987, Wilkins et al. 2006).

The black-capped vireo is vulnerable to brown-headed cowbird parasitism because they accept cowbird eggs (Grzybowski 1995), meaning they do not remove cowbird eggs from the nest and continue to raise the cowbird young. Cowbird eggs usually hatch several days before black-capped vireo eggs and cowbirds are larger than black-capped vireos which allow cowbird nestlings to outcompete black-capped vireo nestlings for food (Grzybowski 1995). Host young almost never fledge from parasitized nests (Wilkins et al. 2006). Black-capped vireos also abandon parasitized nests at a relatively high rate compared to unparasitized nests (Wilkins et al. 2006). At the time of listing, black-capped vireos were frequently parasitized with an approximate parasitism rate of 80% across several study sites (Wilkins et al. 2006). Recent research reports the parasitism rate to range from 12-100% 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 the parasitism rate (Wilkins et al. 2006), but control only takes place over a small percentage of the black-capped vireo range. Describing parasitism in black-capped vireos and identifying how different factors influence brown-headed cowbird parasitism would aid in management and recovery of this species.

One factor that could be related to parasitism is the grazing system where a nest is located. Over 80% of the black-capped vireo breeding range is managed for livestock (Wilkins et al. 2006) and game ranching is also common in some parts of the vireo range

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(personal observation). Much of the land is distinguished into either a *grazed* system (enclosed and sometimes free-roaming ungulates) or a *wild ungulate only* system (only free-roaming ungulates). In a similar situation in New Mexico, Goguen and Mathews (2000) found parasitism of plumbeous vireos (*Vireo plumbeous*) to be 81% in grazed systems and 60% in wild ungulate only systems. Goguen and Mathews (2001) found that 98% of cowbird foraging observations were in association with enclosed cattle or horses in grazed systems rather than with wild elk in wild ungulate only systems which may partially explain the difference in parasitism. Though cowbirds use wild ungulates for foraging, I speculate they prefer enclosed ungulates because their locations are more predictable. Thus, it is important to understand differences in abundance of cowbirds and probability of parasitism in grazed and wild ungulate only systems.

Another factor that could be related to parasitism is the amount of grazing in the landscape because cowbirds are known to regularly commute between foraging and breeding areas (Rothstein et al. 1984, Thompson 1994, Curson et al. 2000). Telemetry studies indicate the average commute is between 1.2 and 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 cowbird foraging area in the landscape 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).

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Grazing intensity is another factor that could be related to brood parasitism. I define grazing intensity as the frequency and duration of grazing. Areas with high grazing intensity would be grazed relatively often and for a relatively long period of time compared to areas with low grazing intensity. Coker and Aspen (1995) found that cowbirds were most abundant in areas where the concentration of livestock grazing areas was highest. Kostecke et al. (2003) found that a reduction in stocking rate from 752 to 103 animal units (0.08 to 0.01 animal units/ha) was associated with reduced parasitism rates in black-capped vireos.

Though grazing related factors may have a large effect on probability of parasitism, it is necessary to investigate whether other factors are influential. The nest concealment hypothesis (also termed the nest exposure hypothesis) states better concealed nests have a lower chance of being parasitized because cowbirds will have a more difficult time finding them and vice versa (Hauber and Russo 2000, Saunders et al. 2003, Fiorini et al. 2012). Some studies indicate nest concealment is an important factor in determining probability of parasitism of songbirds (Burhans 1997, Saunders et al. 2003, Sharp and Kus 2006) while 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 related to probability of parasitism.

OBJECTIVES

Objective 1: Describe cowbird parasitism in black-capped vireos and compare nest site characteristics relative to parasitism status.

Objective 2: Determine whether implementation of grazed systems (enclosed ungulates) or wild ungulate only systems (no enclosed ungulates) influences parasitism and cowbird abundance.

Hypothesis: Probability of brown-headed cowbird parasitism of black-capped vireos and cowbird abundance will be highest in grazed areas and lowest in wild ungulate only areas because enclosed ungulates will attract more cowbirds than wild, free-roaming ungulates.

Objective 3: Determine how grazing in the landscape influences parasitism by using grassland land cover type to represent grazed area.

Hypothesis: Probability of brown-headed cowbird parasitism of black-capped vireos will be highest in areas with a high proportion of grazing in the landscape and lowest in areas with a low proportion of grazing in the landscape.

Objective 4: Determine how grazing intensity influences parasitism by using distance from a nest to the nearest ungulate water source to measure grazing intensity.

Hypothesis: Probability of brown-headed cowbird parasitism of black-capped vireos will increase as grazing intensity increases.

Objective 5: Determine how nest concealment influences parasitism in black-capped vireos.

Hypothesis: More concealed nests will be parasitized less often than less concealed nests because cowbirds will have a more difficult time finding them.

STUDY AREA

I conducted my research on public and private lands in Real, Bandera, Kerr, and Edwards counties, Texas, (Fig. 1) located in the Edwards Plateau ecoregion and within recovery region 2 of the black-capped vireo (Wilkins et al. 2006). Proportion of primarily grazing land ranges from approximately 60% to 80% in each county of my study area (National Agriculture Statistics Service 2007). Free-roaming white-tailed deer, axis deer (*Axis axis*), aoudad (*Ammotragus lervia*), and wild hogs (*Sus scrofa*) are common (personal observation). Private landowners use high fencing (not passable by any ungulate) to enclose their ungulates or traditional low fencing (passable by some ungulates but not others) and land features (i.e. a cliff). These enclosures divide the land into two typical grazing systems: 1) Grazed - *enclosed* livestock (cattle, goats, horses), American bison, and/or exotic game *and* sometimes wild ungulates present (white-tailed deer, axis deer, aoudad, feral hogs); and 2) Wild ungulate only - *no enclosed* ungulates, only wild, free-roaming ungulates present (white-tailed deer, axis deer, aoudad, feral hogs).

My study area is comprised 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 rigidiseta*), and prickly pear (*Opuntia* spp.). From 1992-2011, average monthly precipitation from March to July was

approximately 6.6 cm (National Oceanic and Atmospheric Administration 2014). In

2012 and 2013, average monthly precipitation from March to July was approximately

5.4 and 6.4 cm, respectively (National Oceanic and Atmospheric Administration 2014).

From 1992-2011, average monthly temperature from March to July was 22.2º Celsius

(C) (National Oceanic and Atmospheric Administration 2014). In 2012 and 2013,

average monthly temperature from March to July was 22.9º C and 21.7º C, respectively

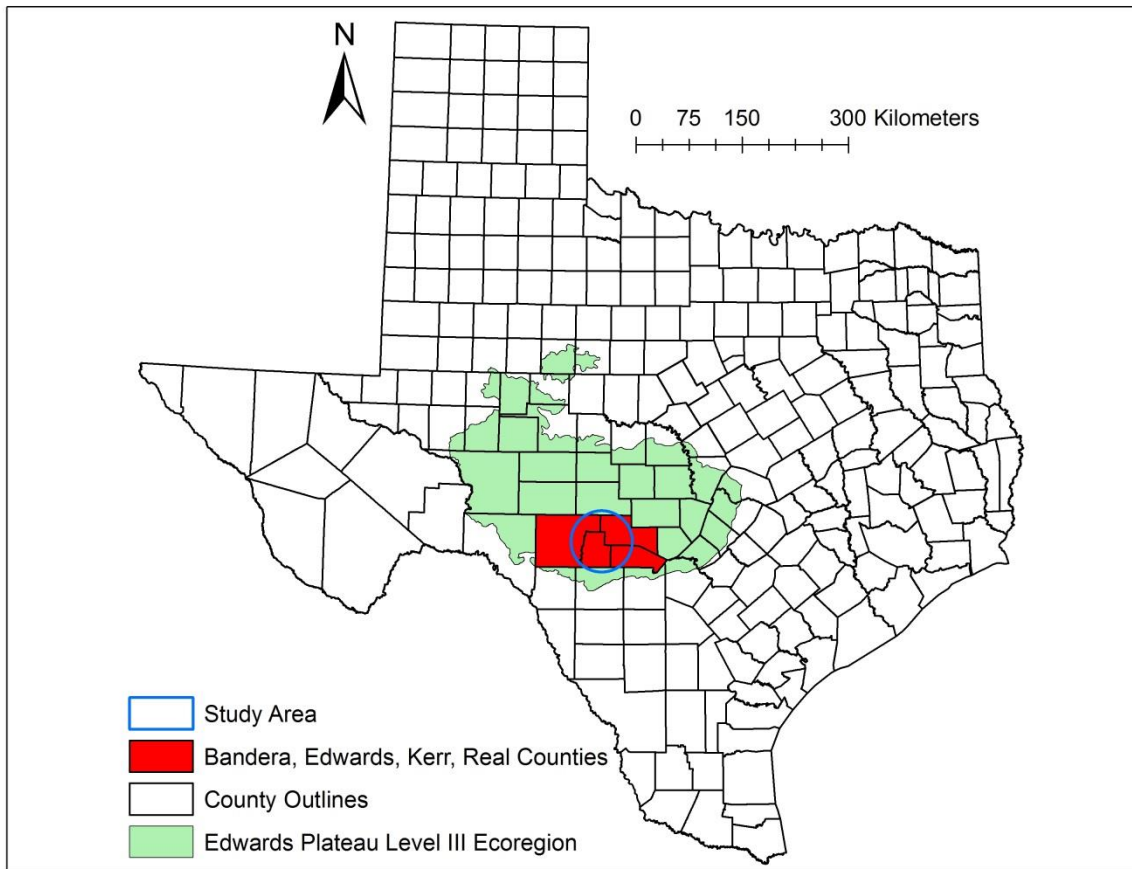(National Oceanic and Atmospheric Administration 2014).

Figure 1. The 2012-2013 black-capped vireo study area located within the Edward's plateau level III ecoregion.

METHODS

Site Selection

McFarland et al. (2013) randomly surveyed some parts of my study area for black-capped vireos. I randomly selected properties where they detected black-capped vireo to request property access. Some previously accessed properties did not grant me access. After exhausting all properties with detections, I selected properties with potential black-capped vireo habitat by randomly selecting a property owner name and then visually scanning aerial imagery of the property for potential black-capped vireo habitat. Each accessible property with vireo detections or unsurveyed property with potential vireo habitat became a potential site. At each potential site, I surveyed for black-capped vireos by listening and watching for them while systematically walking transects 200 m apart, placed in potential habitat. I determined the length of each transect by the extent of potential habitat. I surveyed each potential site 2 to 3 times between 25 March and 21 April in 2012 and 2013. If I did not detect a vireo, I did not select the potential site for study and I surveyed alternative potential sites. If I detected at least one male vireo and it remained territorial, I selected the potential site for study. Levels of parasitism had never been measured at any of the study sites I selected.

My sites were typically > 3 km apart, but my nearest sites were 1 km apart. I had 7 sites in 2012 and 6 sites in 2013. I eliminated one site from the analysis because there was a brown-headed cowbird trap 930 m from the nearest nest and was potentially affecting parasitism probability. This left 12 total sites, six per year. In the 12

remaining sites, there were no cowbirds trapped within 2 km of a nest in the year I collected data.

Nest Searching and Monitoring

After detection, I mapped territories by following male black-capped vireos at a distance of 20 m and marking GPS points. I visited each territory every 2-10 days between sunrise and 7 hours after sunrise; territory visits lasted a maximum of 60 minutes per day. If there were more than 24 territories at a site, I randomly chose a subset of territories to monitor.

I used territory delineations as a guide for nest searching. I located nests through behavioral observations and by vegetation searching. After I located a nest, I monitored it every 2-4 days until the nest was no longer active. I used direct observation, a nest mirror, or binoculars to determine the contents of the nest. If the timing was appropriate for fledging, and nestlings were not in the nest, I searched the territory for fledglings and adults. I determined nests to be successful if I observed a fledgling or adult carrying food, if I heard begging calls, or if an adult was extremely defensive (bill snapping, extreme shradding) near the nest. I only considered nests observed with contents (at least one egg or nestling) for analysis. I considered a nest parasitized if I observed it with contents and at least one egg or nestling was a brown-headed cowbird. I considered a nest unparasitized if I observed it with contents that were all black-capped vireo. After a nest was no longer active, I documented the location of the nest using a GPS unit.

Point Counts

I assessed abundance of cowbirds by randomly placing 12 points spaced >200 m

apart at each site and conducting 5 minute point counts. I conducted point counts three

times during the breeding season approximately 1 month apart (once in April, May, and

June). I counted all female and male cowbirds noting distance and bearing. I conducted

point counts between sunrise and 7 hours after sunrise. I did not conduct point counts

during inclement weather.

Nest Vegetation/Concealment

I measured nest vegetation at all nests that I observed with contents using the

following variables: nest height, substrate species, distance from nest to nearest edge of

woody vegetation, and maximum diameter of woody vegetation where the nest was

located. I also measured nest concealment (percent visual obstruction) from 1 m away at

6 sides (each cardinal direction, above and below). I averaged the 6 estimates of percent

visual obstruction to represent nest concealment. I used a coverboard to measure percent

cover at the nest for 20 height classes (0.1 m intervals) between 0–2 m, estimated 7 m

from the nest in each cardinal direction. I estimated percent visual obstruction for each

section of the coverboard and averaged the 80 estimates to represent percent cover.

I predicted that higher nests and nests closer to the edge of woody vegetation

would be less concealed and parasitized more often because they would have less

vegetation between the nest and a perching cowbird. I also predicted that nests in a

woody vegetation patches with a larger maximum diameter would be better concealed

and parasitized less often because larger woody vegetation patches would have more

woody vegetation concealing nests. I predicted that nests with more concealment and cover would be parasitized less often because these measurements would reflect visual obstruction of the nest.

Grazing in the Landscape

I uploaded nest GPS points into ArcGIS 10.0 and created 3 km radius buffers using the buffer tool to serve as the landscape around nests. Since the typical commute of a cowbird ranges between approximately 1.2 km and 3.0 km (Thompson 1994, Gates and Evans 1998, Goguen and Mathews 2001, Kostecke et al. 2003), I chose a 3 km radius to represent grazing in the landscape because no cowbird telemetry research has been conducted in my study area and it is safer to include potentially unimportant landscape than to exclude potentially important landscape. In addition, the nearest telemetry study to my study area (~200 km away) found the average cowbird commute was approximately 3 km (Kostecke et al. 2003). If the commuting distance was similar in my study area, I would potentially capture the influence of grazing in the landscape on most cowbirds because their commuting distance would be within my radius. In addition, Campomizzi et al. (2013) did not find a relationship between woody cover (essentially the inverse of my grazing in the landscape variable) within 500 m of a nest and parasitism in black-capped vireos; they suggested they may not have found a relationship because their radius was too small and future research could use a larger area. I followed their suggestion. If I had used other radii, the amount of grazing in the landscape would have likely been correlated because one circle would encompass the

other. If I chose a moderately larger or smaller radius, it likely would not have affected my results.

I acquired the 2012 National Agriculture Imagery Program (NAIP) 1 m spatial resolution aerial photos of the area covered by the 3 km buffers. 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, I classified the imagery using the supervised maximum likelihood method into four classes: grassland, woody (trees and shrubs), water, and bare (pavement, gravel roads, unvegetated areas). I assessed the accuracy of my classification by comparing 256 reference points to my classified image and creating a confusion matrix. I established the reference points by randomly placing 200 points over the classified image and then assigning each point a true class by interpreting Google Earth imagery. Upon completion, I only had a total of 4 points in the bare and water classes, so I added 56 points so that each class had at least 30 points. To calculate the proportion of grazing in the landscape around each nest, I divided the area of grassland by the total area of the 3 km buffer.

I chose to represent grazing in the landscape by proportion of grassland because separating this large of an area into grazed and wild ungulate only systems was not possible with available remotely sensed data. Also grassland is a major foraging vegetation type of brown-headed cowbirds (Morris and Thompson 1998, Goguen and

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Mathews 2001) and most of the grassland in my study area is likely grazed by some type of ungulate because of the prevalence of wild ungulates (personal observation).

Grazing Intensity

I chose distance to the nearest ungulate water source to represent grazing intensity under the assumption grazing would be more intense near water since ungulates must return to watering points regularly to stay hydrated. My assumption is supported by studies that found horses (Girard et al. 2013), cattle (Kaufmann et al. 2013), and female white-tailed deer (Brunjes et al. 2006) prefer habitat close to water. Water sources were any type of water that remained for the entire breeding season, including water troughs, ponds, or rivers. Using a GPS unit, I recorded water that landowners informed me of and any water encountered during the course of fieldwork. Additionally, I used my classified image to extract polygons of areas covered by water. Because my classified image was 84.4% accurate (see results), I also visually scanned the aerial imagery for any water that was not accounted for using the preceding three methods. I combined all of this information to form a single polygon layer in ArcGIS 10.0. Using my water source polygon layer, I created another file using the Euclidean distance tool which covered the study area, where every pixel contained the distance to the nearest water. I then extracted this value to each nest point giving the distance to the nearest water.

Time of Nest Initiation - First Egg Ordinal Date

Time of nest initiation affects probability of parasitism in black-capped vireos (Campomizzi et al. 2013) and other songbirds (Rivers et al. 2010, Stumpf et al. 2012).

To control for time of nest initiation in my modeling approach, I 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), so I used a 15 day incubation period and an 11 day nestling period to backdate. If the nest was parasitized and in nestling stage, I used an 11 day incubation period and 10 day nestling period to backdate because brown-headed cowbirds incubation period is 10-12 days and nestling period is 8-13 days (Lowther 1993). If nest check data revealed variation to these period lengths for individual nests, I refined the first egg date estimation accordingly. If I found an active nest with a full clutch, but it failed before I observed hatching, I still backdated to the first egg date by subtracting the median amount of possible days since the first egg was laid from the last date the nest was known to be active.

Data Analysis

I compared the parasitism rate of grazed and wild ungulate only grazing systems using a two-sample test for equality of proportions (Ott and Longnecker 2010:507-513). I compared characteristics of parasitized and unparasitized nests using a t-test when data was normally distributed and a Kruskall-Wallis test when data was not normally distributed (Ott and Longnecker 2010:297-305, 428-436).

To assess relative influence of factors on parasitism, I used an information-theoretic approach (Aikaike's Information Criterion adjusted for small sample sizes, AIC_c; Anderson 2008). I used Program R 3.0.2 (R core development team 2013) to create logistic regression models using the link logit function with a binary response

variable, parasitized or unparasitized. I included an ordinal date of first egg predictor variable for all models because time of nest initiation affects probability of parasitism in black-capped vireos (Campomizzi et al. 2013) and other songbirds (Rivers et al. 2010, Stumpf et al. 2012). I evaluated evidence of mulitcollinearity using variance inflation factors (VIFs) of the global model. I used a Hosmer–Lemeshow goodness-of-fit test to assess goodness of fit of the global model (Hosmer and Lemeshow 2000).

To predict parasitism, I considered four hypotheses: the grazing system hypothesis, the grazing in the landscape hypothesis, the grazing intensity hypothesis, and the nest concealment hypothesis. I represented each grazing related hypothesis with one predictor variable and the nest concealment hypothesis with five predictor variables (Table 1). I divided my model evaluation into two stages; in the first stage, I determined which nest concealment hypothesis variables predict parasitism and in the second stage, I evaluated all hypotheses.

For the first stage, I ran five models each with one respective nest concealment hypothesis predictor variable and the ordinal date of first egg predictor variable. I also ran a null model with only the ordinal date of first egg predictor variable. If a model ranked above the null and within 2 ΔAIC_c of the best model, I included that model in my multi-hypothesis model evaluation to represent the nest concealment hypothesis.

For the second stage of my model evaluation, I constructed 11 models from *a priori* hypotheses (above) about factors that potentially influence parasitism. I included additive terms for my grazing hypotheses variables and the nest concealment hypothesis variable that met my criteria for inclusion. In one model, I included an interaction term

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of grazing system and grazing in the landscape to assess whether the presence of enclosed ungulates was prerequisite for grazing in the landscape to be influential. I also included models with an interaction term of the nest concealment variable and each grazing variable to assess, under the assumption grazing predicts cowbird abundance, if the abundance of cowbirds controls the influence of nest concealment (e.g. if an area has high abundance, nest concealment may not matter because nests are in high demand, and if an area has low abundance, cowbirds may more often find less concealed nests). I also included a model with an interaction term of grazing system and grazing intensity to assess if the presence of enclosed ungulates is prerequisite for grazing intensity to be influential. I considered models with $\Delta AIC_c < 2$ as plausible best models (Burnham and Anderson 2002). Using all models, I report model averaged coefficient estimates and 95% unconditional confidence intervals (Anderson 2008) which I used to evaluate the significance of the variable. I used the best fit model to predict probability of parasitism.

To calculate the average number of cowbirds detected per point, I divided the number of cowbirds detected by the number of point count surveys. I compared the average number of cowbirds detected per point in grazed systems and wild ungulate only systems using a Kruskall-Wallis test (Ott and Longnecker 2010:428-431) because the distribution was not normal.

Table 1. (a) Nest concealment hypothesis, (b) grazing hypotheses, and (c) temporal variables included in logistic regression models predicting probability of parasitism of black-capped vireo nests in Bandera, Edwards, Kerr, and Real counties, TX, 2012-2013.

Variable	Definition (units)
(a) Nest Concealment Hypothesis	
Nestht	Height of nest (m)
Dist_edge	Distance from nest to nearest edge of woody veg. clump (m)
Concealment	Average of percent nest concealed from 1 m at 6 sides (%)
Maxdiam	Maximum diameter of woody veg. motte (m)
Cover	Average of percent height class covered (%)
(b) Grazing Hypotheses	
Graz_intensity	Distance to the nearest ungulate water source (m)
Graz_landscape	Proportion Grassland w/in 3 km of nest (%)
System	Grazed or wild ungulate only grazing system
(c) Temporal	
Ordate	Time of nest initiation - ordinal first egg date (days)

Description

I located 166 nests from 100 territories in 2012 and 216 nests from 104 territories in 2013 for a total of 382 nests. I found 65% of nests early in the nesting sequence (building, laying or within 4 days of the onset of incubation; Mathewson et al. 2012). The earliest first egg date was 3 April in 2012 and 7 April in 2013. The latest first egg date was 27 June in 2012 and 5 July in 2013. See appendix A for details on nest substrate frequency. The overall parasitism rate was 31% ($n = 382$; 2012: 30%, $n = 166$, 2013: 31%, $n = 216$). I observed 9% (2012: 6%, $n = 50$, 2013: 12%, $n = 68$) of parasitized nests to contain 2 cowbird eggs or nestlings. I did not observe any parasitized nests with > 2 cowbird eggs. Adult vireos abandoned 4% ($n = 264$) of unparasitized nests versus 29% ($n = 118$) of parasitized nests. Apparent nest success was 30% ($n = 166$) in 2012 and 27% ($n = 216$) in 2013. Over both years, 6 of 118 parasitized nests (5%) fledged ≥ 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 from the nest while vireo young survived ($n = 2$). Excluding abandoned nests, 53% ($n = 253$) of unparasitized nests were predated while 63% ($n = 84$) of parasitized nests were predated.

Statistical Hypothesis Testing

Nests located in grazed systems had a 39% ($n = 181$) parasitism rate, while nests located in wild ungulate only systems had a 23% ($n = 201$) parasitism rate (chi-square: *P*

= 0.001, χ^2 = 11.198, df = 1; Fig. 2). For nest height, parasitized nests were 23% higher than unparasitized nests which was a statistically significant difference (Table 2) and consistent with the nest concealment hypothesis. Parasitized nests were 16% farther from the nearest edge of woody vegetation clump than unparasitized nests, a difference contrary to the nest concealment hypothesis (Table 2). Parasitized nests were 4% less concealed than unparasitized nests but this difference was not statistically significant (Table 2). Parasitized nests were located in woody vegetation clumps that had a 12% longer maximum diameter than unparasitized nests, differing counter to the nest concealment hypothesis. Parasitized nests had 6% less cover than unparasitized nests, but this difference was not statistically significant (Table 2). Parasitized nests were 7% farther from the nearest ungulate water source than unparasitized nests, a difference opposed to my grazing intensity hypothesis (Table 2). The average first egg date for parasitized nests was 15 days later in the season than unparasitized nests, a statistical difference (Table 2). Overall accuracy of the image classification was 84.4%. See Appendix B for a confusion matrix detailing producer and user class accuracies. Parasitized nests had 20% more grazing in the landscape than unparasitized nests, a statistical difference (Table 2) and consistent with my hypothesis.
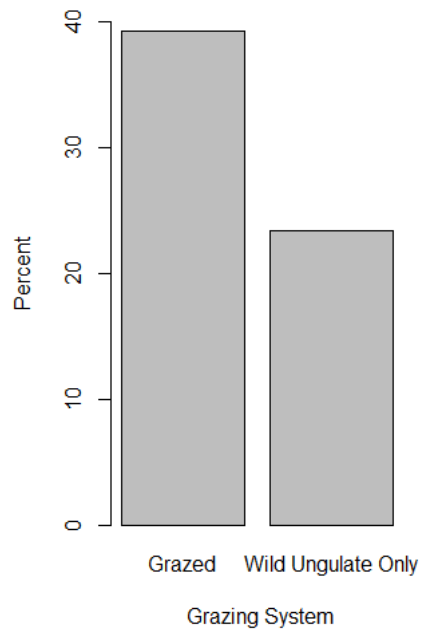
Figure 2. Brown-headed cowbird parasitism rate of black-capped vireo nests in grazed systems (enclosed ungulates) and wild ungulate only systems (no enclosed ungulates) in Bandera, Edwards, Kerr, and Real counties, TX, in 2012 and 2013.

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Table 2. Nest site characteristics with means, standard deviations (St. Dev.), sample size (*n*), and tests of statistical difference for parasitized and unparasitized black-capped vireo nests monitored in Bandera, Edwards, Kerr, and Real counties, TX, 2012-2013.

Nest Variable (units)	Parasitized			Unparasitized			Statistical Tests		
	Mean	St. Dev.	*n*	Mean	St. Dev.	*n*	P-value	Test Statistic	DF[d]
Nestht (m)	1.32	0.72	118	1.07	0.58	264	0.002	[a]9.655	1
Dist_edge (m)	2.09	3.06	118	1.80	1.92	264	na[c]		
Concealment (%)	39.0	18.3	118	40.6	17.8	264	0.432	[b]0.787	380
Maxdiam (m)	19.1	20.2	118	17.1	20.8	264	na[c]		
Cover (%)	69.3	20.0	118	73.5	16.8	264	0.099	[a]2.723	1
Graz_intensity (m)	748.5	353.3	118	701.1	407.8	264	na[c]		
Ordate (day)	145.1	22.0	105	131.1	23.6	259	< 0.001	[a]26.657	1
Graz_landscape (%)	53.6	15.8	118	44.7	15.2	264	< 0.001	[a]20.249	1

[a]Kruskall-Wallis test (χ^2)

[b]T-test (*t*)

[c]Values of means differed in the opposite direction of my hypothesis, making a statistical test unnecessary.

[d]Degrees of freedom

Model Evaluation

I could not estimate ordinal first egg date for 18 nests, so I reduced the dataset to 364 nests for model evaluation. The global model did not show evidence of lack of fit (H-L 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 3), so this was the only variable I used in construction of multi-hypothesis models. In my multi-hypothesis model evaluation (second stage), the best model included an interaction term for system and grazing in the landscape (Table 3). No other models were competitive for the best model ($\Delta AIC_c > 2$). The model averaged coefficient estimate and unconditional confidence interval indicated a significant interaction between system and grazing in the landscape because the model averaged coefficient did not overlap 0 (Table 4). In wild ungulate only systems, the best model predicted relatively low probability of parasitism with similar predicted probability across different amounts of grazing in the landscape (Fig. 3). In grazed systems, the best fit model predicted relatively low probability of parasitism when the amount of grazing in the landscape was relatively low and it predicted relatively high probability of parasitism when the amount of grazing in the landscape was high (Fig. 3).

Table 3. Evaluation of logistic regression models predicting brown-headed cowbird parasitism of black-capped vireo nests for the (a) nest concealment hypothesis and (b) grazing system, grazing in the landscape, grazing intensity, and nest concealment hypotheses. Nests monitored in Bandera, Edwards, Kerr, and Real counties, TX in 2012-2013.

Model[a]	K[b]	AICc[c]	ΔAICc[d]	w_i[e]	LL[f]
(a) Nest Concealment Hypothesis Models					
Nestht	3	413.93	0.00	0.44	-203.93
Null	2	416.00	2.07	0.16	-205.98
Concealment	3	416.01	2.09	0.16	-204.97
Cover	3	416.34	2.42	0.13	-205.14
Dist_edge	3	417.88	3.95	0.06	-205.91
Maxdiam	3	418.03	4.11	0.06	-205.98
(b) Multi-hypothesis Models					
System * Graz_landscape	5	394.88	0.00	0.59	-192.36
Graz_landscape	3	397.21	2.32	0.19	-195.57
Graz_landscape * Nestht	5	397.75	2.87	0.14	-193.79
System + Graz_landscape	4	399.20	4.31	0.07	-195.54
System * Nestht	5	404.06	9.18	0.01	-196.95
Graz_intensity * Nestht	5	406.96	12.08	0.00	-198.40
System	3	407.63	12.74	0.00	-200.78
System * Graz_intensity	5	410.62	15.74	0.00	-200.23
Nestht	3	413.93	19.04	0.00	-203.93
Null	2	416.00	21.12	0.00	-205.98
Graz_intensity	3	416.76	21.88	0.00	-205.35

[a]All models include a time of nest initiation variable, models with an interaction term (with a "*") include additive terms for each variable.
[b]Number of parameters.
[c]Akaike's Information Criterion values, corrected for small sample size.
[d]Difference between AICc value of current model and most-supported model.
[e]Relative likelihood the model is the best model.
[f]Log Likeliehood

Table 4. Model averaged coefficients and 95% unconditional confidence intervals from models predicting cowbird parasitism of black-capped vireo nests from Bandera, Edwards, Kerr, and Real counties, TX in 2012-2013.

Variable	β[a]	CI[b]
Nestht	0.3739	0.0106, 0.7373
Graz_intensity	0.0003	-0.0003, 0.0009
Graz_landcape	3.6670	1.7939, 5.5402
System	0.0758	-0.6890, 0.8406
System * Graz_landscape	-6.7872	-12.0509, -1.5235
Graz_landcape * Nestht	2.3352	-0.5034, 5.1739
System * Nestht	-0.9980	-1.8630, -0.1329
Graz_intensity * Nestht	0.0017	0.0005, 0.0029
System * Graz_intensity	-0.0002	-0.0014, 0.0010
Ordate	0.0236	0.0128, 0.0344

[a]Model-averaged coefficient
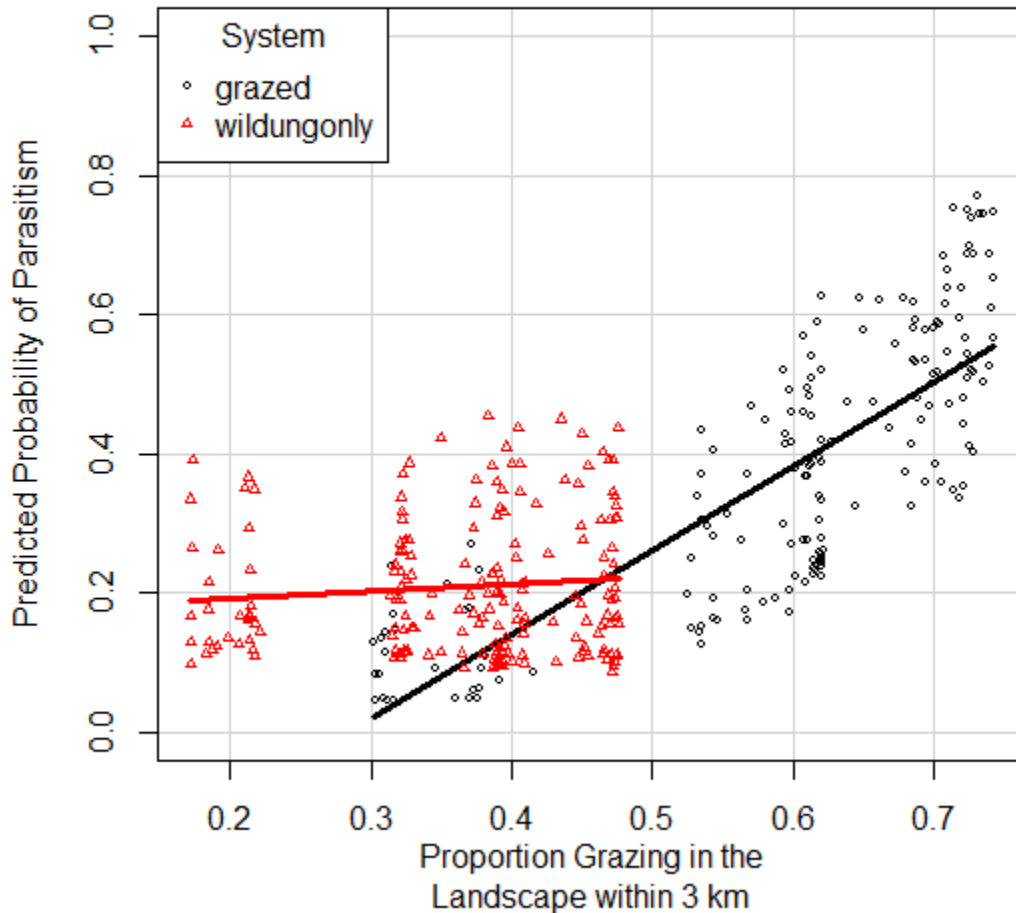[b]95% unconditional confidence interval

Figure 3. Predicted probability of cowbird parasitism of black-capped vireo nests plotted against the proportion of grazing in the landscape within 3 km of nests for grazed systems (black circles) and wild ungulate only systems (red triangles). I used the best fit logistic regression model to predict probability of parasitism of a nest, based on nests monitored in 2012-2013 in Bandera, Edwards, Kerr, and Real, counties, TX.

Point Counts

In both 2012 and 2013, I conducted 108 point count surveys in each grazing system (grazed and wild ungulate only), for a total of 216 per system. I detected 34 (2012: 7, 2013: 27) brown-headed cowbirds at grazed sites and 13 (2012: 9, 2013: 4) at

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wild ungulate only sites. The average number of cowbirds detected per point count was higher at grazed sites (mean = 0.16, sd = 0.49) than at wild ungulate only sites (mean = 0.06, sd = 0.24; K-W: $P = 0.035$, $\chi^2 = 4.436$, df = 1).

DISCUSSION AND CONCLUSIONS

The influence of grazing in the landscape on probability of parasitism depended on the grazing system; grazing in the landscape did not influence probability of parasitism in wild ungulate only systems, but did influence parasitism in grazed systems. Cowbirds should prefer the closest available breeding areas to their foraging areas because shorter commutes allow for more energy to be expended on egg production which potentially would increase cowbird fitness (Kostecke et al. 2003). Grazed systems could have provided a reliable source of ungulates and grazing in the landscape may have influenced the number and distribution of cowbird foraging opportunities. Nests located in grazed systems with a high amount of grazing in the landscape would have a higher number of, and likely more distributed, cowbird foraging opportunities leading to higher probability of parasitism because cowbirds would more often have a shorter commute. Wild ungulate only systems may have had relatively low probability of parasitism regardless of grazing in the landscape because reliable foraging opportunities would have to be found elsewhere meaning cowbirds breeding in wild ungulate only systems had to commute farther distances. This increased commute would have lowered egg production and fitness which may have lowered cowbird abundance and lowered the probability of parasitism. The availability and distribution of cowbird foraging areas likely were the underlying mechanisms that influenced parasitism in my study.

My results are in agreement with research that suggests a relationship between variables similar to, or the inverse of, my grazing in the landscape variable 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 while 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, emphasizing the influence of cowbird foraging opportunities on parasitism across different host species and geographic areas. 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 my grazing 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 where a larger area might have had different results because of cowbirds' willingness to commute long distances. My results support their speculation. Campomizzi et al. (2013) also may not have found a link between woody cover and parasitism because they compared its influence against a time of nest initiation variable. Time of nest initiation may have had a large effect relative to woody cover. I also found an influence of time of nest initiation on parasitism; my results show nests are more likely to be parasitized as the breeding season moves forward. In the beginning of the season more birds are initiating nests (both interspecifics and conspecifics) and the high number of nests may dilute parasitism. As the season progresses, fewer nests are

available for the same number of cowbirds, so nests are parasitized more frequently. I included a time of nest initiation variable in all my models because, based on Campomizzi et al. (2013), it has a strong influence on parasitism in black-capped vireos. I was not interested in assessing its influence on parasitism relative to other factors because it cannot be managed.

I detected more cowbirds in grazed systems than wild ungulate only systems supporting my hypothesis that cowbirds are more abundant where there are enclosed ungulates. My result agrees with Goguen and Mathews (2000) who found more cowbirds in grazed systems versus wild ungulate only systems in New Mexico. I speculate cowbirds may be more abundant in grazed systems because the enclosures limit ungulate movement and the location of ungulates may be more predictable. However, if the location of ungulates is important, then cowbird abundance and parasitism could also be related to ungulate type. Wild ungulates such as white-tailed deer spend more of their time in non-grassland areas because they are browsers (Deperno et al. 2002). Enclosed ungulates are often cattle and horses which are grazers and spend more of their time in grassland (Lamoot et al. 2005), cowbirds main foraging vegetation (Morris and Thompson 1998). Unfortunately, I was unable to examine the influence of ungulate type on cowbird abundance or parasitism because my sites had a mixture of ungulate types. Future research could examine the influence of ungulate type on cowbird foraging and parasitism in a tightly controlled situation.

I did not observe an influence of grazing intensity on parasitism. My results are not consistent with Kostecke et al. (2003) who found that parasitism in black-capped

vireos decreased by decreasing grazing intensity. The cause of our contradictory results

could be related to how we assessed grazing intensity and by our study designs. At a

consistent grazed site, Kostecke et al. (2003) observed a reduction in stocking rate (0.08

to 0.01 animal units/ha) and compared parasitism in the pre-reduction time period to

parasitism in the post-reduction time period; parasitism decreased sharply (19-35% to 2-

3%). I did not use stocking rate because some landowners could not accurately provide

it and, in addition to enclosed ungulates already on sites, some landowners added

ungulates to study sites during the vireo breeding season making an estimation of

stocking rate problematic. Instead, I used distance to water to serve as grazing intensity

because some ungulates prefer to be near water (Brunjes et al. 2006, Girard et al. 2013,

Kaufmann et al. 2013) so I assumed they would graze more often there. I also wanted to

estimate grazing intensity in wild ungulate only systems and it was not possible to get a

pseudo-stocking rate at those sites because they were not enclosed. Perhaps I 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. Although I did not observe an effect of grazing intensity, I think in some

situations it does have an influence on parasitism, as Kostecke et al. (2003) suggested.

My results did not indicate an important effect of nest concealment. Its possible

black-capped vireos do not place their nests according to concealment because adult

songbirds incubating nests, and the nests themselves, are vulnerable to predation (Stake

and Cimprich 2003, Reidy et al. 2008, Conkling et al. 2012). Predation may have a

larger influence on nest placement than parasitism so nests are placed to decrease the

likelihood of adult and nest predation. Optimal placement to reduce predation may have

minimal association with nest concealment because most black-capped vireo nest

predation occurs at night (Stake and Cimprich 2003), and some predators may be using

cues besides visual detection. Another reason I did not find an influence of nest

concealment may be because cowbirds' primary nest searching strategy may be by

observing host behavior and not by vegetation searching. My results are mostly

consistent with Barber and Martin (1997) who did not find any difference in nest

characteristics between parasitized and unparasitized black-capped vireo nests. In one

measurement, our results differed; I found a difference in nest height between parasitized

and unparasitized nests and they did not. Despite the statistical difference in nest height,

the effect size was small (0.25 m) and my model evaluation indicated nest concealment

was relatively unimportant in predicting probability of parasitism compared to grazing

related factors.

The overall level of parasitism I 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 I only

observed parasitism in one year per site. I observed low overall parasitism compared to

Farrell et al. (2010; 100%, $n = 20$), and comparable parasitism to Smith et al. (2012;

34% $n = 119$), where both studied in other parts of the vireo range not managed for

cowbirds. I found a low overall parasitism rate compared to Campomizzi et al. (2013;

72% $n = 38$) where cowbird management took place at half of their study sites and I

observed higher parasitism than Pope (2011; 19% $n = 302$) who studied in an area with

cowbird management. My observed parasitism rate was substantially lower than the approximate 80% rate observed across several areas prior to the initiation of cowbird control in Texas in 1988 (Wilkins et al. 2006). Per Wilkins et al. (2006), the variation in parasitism could be partially related to geographic area, since cowbird parasitism of black-capped vireos tends to be higher in the northern and eastern parts of the vireo range (i.e. Farrell et al. 2010, Campomizzi et al. 2013) and lower in the southern and western parts (i.e. Smith et al. 2012). However, from 1985 to 1988, parasitism at one site in Kerr county (southern part of the breeding range) ranged from 65% ($n = 20$) to 90% ($n = 10$) (Wilkins et al. 2006). The moderate parasitism I observed in Kerr and surrounding counties could be partly due to a cowbird population decline in the Edward's Plateau, as observed from 1966 to 2011 through the Breeding Bird Survey population index (Sauer et al. 2012).

My research provides information on brood parasitism of black-capped vireos in areas not managed for cowbirds and where parasitism had never been described before. Such information is important in assessing the vireos status because brood parasitism was a contributing factor to it being endangered. My research also provides suggestions about why parasitism varies which could be useful for land management.

Management Implications

My research suggests cowbird management would be highest priority in grazed systems with a large amount of grazing in the landscape and low priority for wild ungulate only systems and grazed systems with a low amount of grazing in the landscape. It also suggests wild ungulate only systems and grazed systems with a low

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amount of grazing in the landscape would be higher priority for preservation than grazed

systems with a high amount of grazing in the landscape. In grazed systems with a high

amount of grazing in the landscape, managers could encourage grassland to woody

vegetation succession to possibly lower parasitism; similarly, managers could avoid

removing woody vegetation in grazed systems.

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APPENDIX A

Table 5. Nest substrates used by black-capped vireos in Bandera, Edwards, Kerr, and Real counties, in 2012 and 2013.

Common Name	Scientific Name	Count	Percent ($n = 382$)
Agarita	*Berberis trifoliolata*	5	1.3
Ashe Juniper	*Juniperus ashei*	94	24.6
American Sycamore	*Platanus occidentalis*	1	0.3
Black Cherry	*Prunus serotina*	1	0.3
Buckeye	*Aesculus spp.*	2	0.5
Blackjack Oak	*Quercus marilandica*	2	0.5
Evergreen Sumac	*Rhus virens*	1	0.3
Hackberry	*Celtis spp.*	2	0.5
Lacey Oak	*Quercus laceyi*	24	6.3
Live Oak	*Quercus virginiana*	13	3.4
Mountain Laurel	*Sophora secundiflora*	69	18.1
Post Oak	*Quercus stellata*	1	0.3
Redbud	*Cercis canadensis*	1	0.3
Shin Oak	*Quercus sinuata*	63	16.5
Texas Red Oak	*Quercus buckleyi*	4	1.0
Texas Persimmon	*Diospyros texana*	99	25.9

Table 6. A confusion matrix for the image classification derived from 2012 NAIP aerial imagery. The table was created from the classification data and reference data. The classified image encompassed parts of Bandera, Edwards, Kerr, and Real counties that were within 3 km of black-capped vireo nests monitored in 2012-2013.

Classified Category	Actual Category				Total	User's Accuracy
	Bare	Grassland	Water	Woody		
Bare	22	0	0	0	22	100.0%
Grassland	7	73	1	23	104	70.2%
Water	0	0	23	0	23	100.0%
Woody	1	2	6	98	107	91.6%
Total	30	75	30	121	256	
Producer's Accuracy	73.3%	97.3%	76.7%	81.0%		

Overall Accuracy = 84.4% Kappa Coefficient = 0.76