



Management and Conservation

Black-Capped Vireo Nest Predator Assemblage and Predictors for Nest Predation

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ABSTRACT Nest predation is a major limiting factor for songbird productivity, including the federally endangered black-capped vireo (*Vireo atricapilla*). However, nest predator information is limited across the range of the black-capped vireo in central and southwest Texas. We monitored nests in 3 counties within the breeding range of black-capped vireos in Texas in 2008 and 2009 and used continuous recording digital video cameras to record predation events. We video-monitored 115 nests and documented 39 predation events by at least 9 predator species. Overall, we observed avian species (51%, $n = 39$), specifically brown-headed cowbirds (*Molothrus ater*; $n = 12$), and snakes (26%, $n = 39$) as the most frequent nest predators. The estimated daily nest survival rate during the laying and incubation stage was 0.985 (95% CI = 0.967–0.993) and 0.944 (95% CI = 0.921–0.961) during the nestling stage. In addition, we analyzed models of predator-specific nest predation using multinomial logistic regression. Effect of nest height on predation rate was significant for snakes; nest stage was significant for nests depredated by avian predators. By identifying and increasing our knowledge of nest predators and vegetation characteristics associated with greater risk of predation in multiple locations within the black-capped vireo's range, we can effectively manage habitat to benefit recovery efforts of the species. © 2012 The Wildlife Society.

KEY WORDS black-capped vireo, nest camera, nest predation, predators, Texas, *Vireo atricapilla*.

Predation is the leading cause of nest failure in songbirds (Martin 1993, Schmidt and Whelan 1999a). Recent studies of nesting birds have investigated general nest predators or the relationships between predator assemblages (Sovada et al. 2000, Smith et al. 2004) and vegetation type (Kuehl and Clark 2002, Thompson and Burhans 2004, Stake et al. 2005, Marzluff et al. 2007). Predator assemblages also may be altered by different land use practices or fragmentation of the landscape (Chalfoun et al. 2002, Thompson 2007, Sperry et al. 2009), which may be more common in properties managed for private use. Because spatial and temporal patterns of predators may drive reproductive success for avian

species (Sperry et al. 2008, Benson et al. 2010), managers will also benefit by understanding how the local habitat characteristics relate to nest predation by specific predators. This increases our ability to understand and manage for habitat characteristics that are beneficial and increase survival for the species at risk.

Examining the impacts of specific predator classes on avian nest survival (Batáry and Báldi 2004, Benson et al. 2010) is an important step in avian conservation. Until recently, predator identification was based solely on incidental sightings or inferences from remaining nest contents (Martin 1993, Grzybowski 1995, Schmidt and Whelan 1999a), which can lead to inaccurate identification of nest predator species (Williams and Wood 2002). Without the ability to identify major predators, many studies group all predation events together, which may obscure true relationships between predator classes and nest site or landscape characteristics (Wilson and Cooper 1998, Schmidt and Whelan 1999b). Monitoring methods using video cameras for continuous surveillance allow for predator identification (Stake and Cimprich 2003, Thompson and Burhans 2003, Pierce and Pobprasert 2007, Conner et al. 2010). However, even with the increased ability to identify predators, only a few studies have incorporated camera-identified predators with predator-specific analyses of habitat characteristics and nest

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survival (Thompson and Burhans 2003, Benson et al. 2010). If nest site characteristics can predict predator-specific causes of nest failure, these results may have implications for the effectiveness of management strategies, especially for endangered species.

The black-capped vireo (hereafter vireo) is a federally endangered migratory songbird (Ratzlaff 1987) whose numbers have been declining because of habitat loss, habitat fragmentation, and parasitism by brown-headed cowbirds (*Molothrus ater*, Grzybowski 1995). The breeding range for the vireo extends from localized areas in western Oklahoma through central Texas and south to Coahuila, Mexico (Grzybowski et al. 1994, Grzybowski 1995). Typical vireo breeding habitat is characterized by clumps of shrubby, deciduous vegetation of irregular heights commonly less than 3 m; these clumps cover 35–55% of the landscape and vegetation cover usually extends to the ground (Grzybowski et al. 1994, Bailey and Thompson 2007). Vireo habitat in Texas ranges from the Edwards Plateau ecoregion (Grzybowski et al. 1994), which is dominated by multiple *Quercus* spp. and oak-juniper (*Juniperus* spp.) woodlands and interspersed grasslands providing successional habitat, to the western Trans-Pecos ecoregion where xeric shrub vegetation dominates the landscape.

Research on nest predators of vireos previously occurred in Bell and Coryell Counties, Texas. Stake and Cimprich (2003) used a video monitoring system on Fort Hood in east-central Texas to examine nest predators at vireo nests. Texas ratsnakes (*Elaphe obsoleta lindheimeri*) and red imported fire ants (*Solenopsis invicta*) accounted for 38% and 31%, respectively, of predation events on vireo nests, whereas avian predators and mammals were responsible for the remaining nests. Identified predators from other studies include gray foxes (*Urocyon cinereoargenteus*), fox squirrels (*Sciurus niger*), and raccoons (*Procyon lotor*; Grzybowski 1995).

Other than nest video collected at Fort Hood or incidental observations at nests (Graber 1961, Grzybowski 1995), no information exists for vireo nest predation events or nest predators in any other region of the species' range. Given the change in environmental conditions across the range, it is reasonable to expect that the predator assemblage, and thus major limiting factors, may differ depending on location and vegetation type. Our objectives were to: 1) identify nest predators and nest vegetation characteristics of black-capped vireos in different portions of their range in Texas; 2) examine if nest survival can be predicted by habitat or temporal factors; and 3) determine if these predictors are specific to major predator classes.

We examined specific hypotheses regarding the influence of vegetation structure and temporal factors on overall nest survival and predation based on groups of predator species (snakes, ants, birds, and mammals). The nest-concealment hypothesis (Martin 1993) predicts that nest predation risk decreases with increasing vegetation at the nest because of reduction in visual and olfactory cues. Concealment may reduce nest predation, especially during the nestling stage, because many visually oriented predator species may be

attracted to additional activity at the nest from adults feeding nestlings, and nestling activity or noise (Skutch 1949, Lowther 1993, Mullin and Cooper 1998, Curry et al. 2002, Liebezeit and George 2002). Additionally, the edge effect hypothesis proposes that nest success declines with increasing proximity to edge habitat (summarized by Batáry and Báldi 2004). If the major nest predators in a region demonstrate a preference for edge habitat, nests located near these edges may face greater risk of predation.

We made predator-specific predictions for the relationship between predation and nest height, distance to habitat edge, and percent concealment. For most predator groups (birds, mammals, and snakes), we predicted that nest predation would decrease with increasing concealment and distance from the habitat edge, because a reduction in these 2 variables would make locating nests easier for potential predators. We also predicted a positive relationship with distance to edge (but not concealment) for ants, because ants do not rely on visual cues to locate potential prey.

Snakes may use visual cues to locate potential prey and identify active nests (Mullin and Cooper 1998), so increased nest activity associated with feeding nestlings potentially contribute to higher predation by snakes during the nestling stage than during incubation (Eichholz and Koenig 1992, Stake et al. 2005, Benson et al. 2010). Ratsnakes in Texas increase foraging activity as summer progresses, which may also increase nest predation risk (Sperry et al. 2008). However, this mid-summer foraging is restricted to nocturnal periods when temperatures are cooler (Sperry et al. 2010), which may make them less likely to locate nests by visual activity of adult birds (Mullin and Cooper 1998), especially later in the breeding season. Snakes also show a preference for edge habitat or shrubs (Sperry et al. 2009, Klug et al. 2010). If vireos are nesting in highly fragmented habitat (or in small shrub patches) they may be at a greater risk for snake predation.

Avian predators also appear to use visual cues to locate potential prey and identify active nests (Clotfelter 1998, Robinson and Robinson 2001, Hughes 2011) and also may depredate nests that are less concealed and closer to the shrub edge (Liebezeit and George 2002). For example, western scrub-jays (*Aphelocoma californica*), common in our study areas, are opportunistic predators that are known to locate nests based on parental cues and consume both eggs and nestlings of multiple songbird species (Curry et al. 2002). Brown-headed cowbirds are unique in that they are a parasitic-generalist species that remove host eggs (and occasionally nestlings) and lay their own eggs in the host nest (Elliott 1999). Extensive control is required to reduce parasitism levels at vireo nests to <10% (Kostecke et al. 2005). However, that intensity is usually with a large logistical expense, and is not feasible across the majority of the vireo's breeding range.

Additionally, cowbirds also may remove host eggs and host nestlings from nests without subsequent parasitism events, which can result in nest failure (Elliott 1999, Stake and Cavanagh 2001, Stake and Cimprich 2003). Researchers have hypothesized that female cowbirds depredate these

host nests found late in the nesting cycle to induce re-nesting by host species, thus creating future parasitism opportunities (Arcese et al. 1996, Hoover and Robinson 2007, Benson et al. 2010). We expected a decreasing risk of predation for all predator groups except for birds with increasing nest height. Lower nests may be more easily accessible by snakes, mammals, and ants, which are often ground-based predators. Bird foraging behaviors differ from other predator species because they are not restricted to ground level for observing potential prey, thus may be more likely to detect nests from perches within the canopy (Sharp and Kus 2006).

Red imported fire ants, an introduced predator in the southern United States, can swarm and kill nestlings (Kopachena et al. 2000, Stake and Cimprich 2003, Allen et al. 2004, Campomizzi et al. 2009), which can result in decreased nest survival, especially during the nestling stage. Fire ants are commonly found in disturbed areas, including edges (Graham et al. 2008) and forage more frequently at ground level than in vegetation (Campomizzi 2008).

Mammals, although dominant predators in fragmented forests (Stake and Cimprich 2003, Thompson and Burhans 2003, King and DeGraaf 2006), are not a major nest predator in shrub-nesting avian species (Söderström et al. 1998, Schaefer 2004, Thompson 2007). However, regardless of location, mammals appear to use both visual and olfactory cues to locate nests (Whelan et al. 1994), which could increase risk of predation in the nestling stage, or nests lower in the vegetation that are more easily found and accessed by opportunistically foraging mammalian predators.

We also predicted temporal influences on daily nest predation. The risk of nest predation may vary based on time-specific variables including nest initiation date (Bailey 2005, Grant et al. 2005, Sperry and Weatherhead 2009). Previous vireo research in the region indicates a decline in daily nest survival throughout the season (Bailey 2005, Campomizzi 2008). Additionally, both snakes and fire ants show seasonal patterns of activity due to increasing temperatures (Vogt et al. 2003, Sperry et al. 2008, Weatherhead et al. 2010), so we expected a decrease in daily nest survival as the season progressed.

STUDY AREAS

In 2008 and 2009, we studied vireos at study sites in Coryell, Kerr, and Val Verde Counties (2009 only), Texas (Fig. 1). The study sites in Coryell County were located in the Leon River watershed within the Cross Timbers and Prairies ecoregion of the Edwards Plateau and consisted of 11 privately owned properties with active vireo territories detected during previous presence-absence surveys on 33 properties within 140,000 ha. Study sites in Coryell County ranged from 36 ha to 103 ha and included mid-successional woody vegetation, mixed grassland and mature oak-juniper woodland, and nearby mature oak-juniper woodland, similar to habitat occupied by other vireo populations in the area (Grzybowski et al. 1994, Bailey and Thompson 2007). Proximity from study sites to the boundary of Fort Hood ranged from 1 km to 15 km. The topography consisted of rocky limestone hillsides and mesas ranging in elevation from

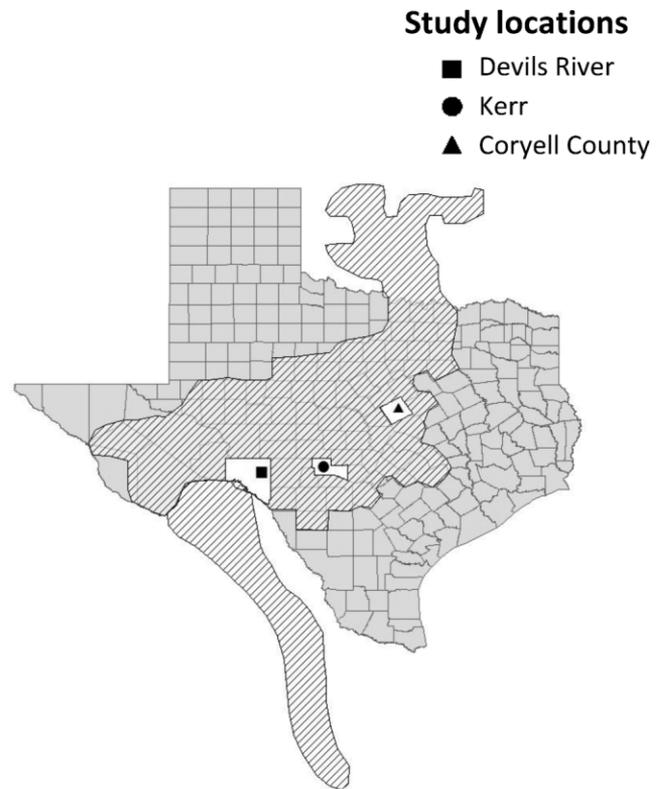


Figure 1. Breeding range of the black-capped vireo (striped; range estimate from Wilkins et al. 2006) and locations of study areas where we conducted monitoring of black-capped vireo nest predators in Coryell County, Kerr County, and Val Verde County, Texas in 2008 and 2009.

200 m to 500 m; primary land uses in the area were ranching, hunting, and farming. Additionally, 8 (of the 11) private properties also had localized trapping efforts for brown-headed cowbirds, with 33 traps capturing 56 cowbirds (22 females) per trap in 2008 and 34 cowbirds (11 females) per trap in 2009. Although these efforts substantially reduced parasitism compared to nontrapped properties from 2007 to 2009 (67%, $n = 37$), rates in Coryell County still averaged 31% ($n = 29$; M. L. Morrison, Texas A&M University, unpublished data).

In 2008 and 2009, we studied vireos in Kerr County at Kerr Wildlife Management Area (WMA) and 5 private properties nearby (hereafter Kerr). Publicly owned and managed by the Texas Parks and Wildlife Department, Kerr WMA was located at the headwaters of the North Fork of the Guadalupe River and consisted of 2,628 ha of limestone landscape features typical of the Edward's Plateau ecoregion. Primary land uses were for ecological and wildlife-based research, public access for hunting and wildlife viewing, and limited cattle grazing. All Kerr properties together comprised 8,000 ha. In the Kerr area, 3 vegetation types occupied by vireos were identifiable by topography, soil type, land-use, and previous management practices. Shrubland was composed of oak (or other deciduous species) enclosed in a grassland matrix; deciduous woodlands included taller trees and greater canopy cover, primarily along drainages; and oak-juniper woodland. Primary land uses

in the Kerr area included prescribed burning, cattle grazing, native and exotic hunting, wildlife viewing and recreation, and brown-headed cowbird trapping. In 2008, Kerr WMA operated 9 cowbird traps, with 39 cowbirds (19 females) caught per trap, and in 2009 operated 11 traps with 48 cowbirds (20 females) per trap.

In 2009, we collected data at Devils River State Natural Area (managed by the Texas Parks and Wildlife Department) and Dolan Falls Preserve (managed by The Nature Conservancy) in Val Verde County, Texas (hereafter Devils River). The natural plant communities at Devils River included mesquite-chaparral of the South Texas Plains, oak-cedar of the central Edwards Plateau to the east, and sotol-lechuguilla of the Trans-Pecos to the west (Smith and Butterwick 1975). Devils River covered approximately 8,100 ha and included plateaus containing flat-topped ridges bisected by several large drainage systems creating canyons, dry river washes and stream beds, and lower-elevation flat plains. Vireo habitat included locations on dry rocky slopes (slope habitat) dominated by oak-juniper, legugilla-sotol, and Texas persimmon (*Diospyros texana*); dense oak-juniper communities along dry creek beds and drainages (riparian); and low flat areas at low elevations dominated by cenizo (*Leucophyllum frutescens*), mesquite (*Prosopis glandulosa*), and multiple woody shrubs. Primary land uses in the area were wildlife viewing and recreation (Texas Parks and Wildlife Department 2008). Managers did not actively trap cowbirds at Devils River.

METHODS

Nest Searching and Video Monitoring

We located current and previously active black-capped vireo territories at all study areas through ongoing surveys and historical territory locations and then located vireo nests in each monitored territory using behavioral observations of adult birds and systematic search techniques (Ralph et al. 1991, Martin and Geupel 1993) from March to July 2008 and 2009. We used a continuously recording video camera system to accurately identify predators and nest fate. The system consisted of a weatherproof bullet camera with a 3.6 mm lens and infrared lighting (Rainbow, Costa Mesa, CA) to record predation events 24 hour a day. We placed the video camera near enough to the nest to capture all activity, but not disturb the birds (>1–2 m). A 15-m cable connected the camera unit to a digital video recorder (DVR; Detection Dynamics, Austin, TX) and a 12-V 26-A-hr battery (Batteries Plus, Hartland, WI). For 2009, we supplemented battery power with 20-W solar panels (Suntech, San Francisco, CA). We used a time-lapsed recording of 5 frames per second to maximize data storage on the DVR.

In Coryell County, we had a low abundance of breeding vireos, so we attempted to place cameras on every active vireo nest. At Kerr and Devils River, we prioritized camera placement on nests based on availability of camera units and stratified distribution of cameras on nests throughout available vegetation types (shrubland, juniper woodland, and deciduous woodland at Kerr; low flats, slopes, and riparian

areas at Devils River) to ensure that monitored nests represented available nests at the study sites. If multiple nests were available within each habitat, we preferentially chose nests earlier in the nesting cycle (i.e., day 2 of incubation vs. day 12) to maximize the amount of video footage for each stage to identify nest predators without biasing the sample towards predation occurring later in the nesting cycle. Additionally, we also monitored vireo nests without cameras at all study areas, but these results are presented elsewhere (Conkling 2010, Pope 2011, Smith et al. 2012).

For all nests, we placed cameras only after incubation had commenced (defined as the day the adult laid the last egg in the nest) or after we determined the adults were incubating based on behavior and nest contents. For nests found during the nestling stage, we placed cameras only if the nestlings were <6 days old to minimize the risk of force-fledging the nestlings. We observed nests for up to 1 hour following camera placement to determine that birds did not abandon nests as a result of camera placement; observations ceased once the adult(s) returned to the nest and resumed incubation or nestling care. We checked the camera system every 2–3 days to replace data cards and batteries and left the camera in place until the nest fledged or failed. We visually checked nests every 2–7 days because not all camera positions allowed full view of the nest interior. Furthermore, these observations helped us to determine which video segments we needed to view to identify predators. For nests found during the nestling stage, we aged nestlings based on progression of physical development. If a nest was parasitized, we added the cowbird egg to prevent hatching and returned it to the nest. We considered all nests that fledged host or cowbird offspring as successful because our goal was to examine predation and we assumed that the species of young in the nest would not alter the likelihood of predation.

We defined a predation event as the removal or consumption of ≥ 1 egg or nestling from a nest by a species other than vireos, including partial predation events. We did not consider nest abandonment by adults even if associated with nest visitation by another species unless nest contents were removed. For example, 1 nest was abandoned because a gray fox (*Urocyon cinereoargenteus*) rested under the nest for 4 hours; however, we did not consider this a predation event because the fox did not appear to notice the nest. Similarly, we did not consider parasitism by cowbirds as a predation event unless the cowbird concurrently removed an egg or nestling. Furthermore, we only considered cowbirds as predators when they removed nest contents after the initiation of incubation because we did not have video footage during the laying period.

If we observed a loss of eggs or nestlings between consecutive nest checks, we viewed all nest video footage during that period to determine if the loss resulted from weather-related events, nest disturbance, or predation and, if observed, to identify the nest predator. We watched all video footage after the last visual nest check before the nest fledged to determine the fledge date or if any late-nestling predation events occurred. If we observed a predation event, we documented the date, time, and activity of the identified nest predator,

including disturbance or removal of host eggs or nestlings when possible.

Vegetation Sampling

We collected vegetation measurements at each nest location after nests failed or fledged young. Vegetation measurements were nest height, nest substrate, and distance and direction to nearest habitat edge. Because vireos typically nest in distinct shrub clumps (Grzybowski 1995), we measured the distance to habitat edge as the horizontal distance from the nest to the nearest break in contiguous shrub vegetation. We also recorded distance to edge in each of the cardinal directions to quantify the minimum dimensions of the shrub vegetation based on the area of a quadrilateral with diagonals equal to the distance to edge in each of the cardinal directions. We measured concealment from each cardinal direction by recording the total percent area visible at 7 m from 0 m to 2 m above ground on a 2-m profile board placed at the nest (Guthery et al. 1981).

Analyses

We analyzed vegetation data by examining scatter plots and mean values for vegetation characteristics. We used Pearson correlation to test for correlation among vegetation variables and analysis of variance (ANOVA; $\alpha = 0.05$) to compare mean differences between vegetation characteristics among study locations (± 1 SE) using SPSS 15.0 (SPSS Inc, Chicago, IL). We used an information-theoretic approach to evaluate support for models describing daily nest survival (DSR) and predator-specific predation rates for vireo nests. We used the same set of candidate models describing habitat characteristics and within-season temporal factors for both analyses. We did not include the effects of location in the model set for predator-specific predation rates because sample sizes were too small within different predator classes. Furthermore, we expected that predators within each predator class would respond similarly across the range to differences in vegetative characteristics (i.e., we did not predict an interactive effect between geographic location and vegetation characteristics).

We used logistic-exposure to model daily nest survival (DSR) as a function of study location, temporal variables, and vegetation variables (Shaffer 2004, Shaffer and Thompson 2007) using R 2.11.1 (R Development Core Team, Vienna, Austria). Our daily nest survival analyses examined the effect of predictor variables on the overall success of a nest, not considering partial predation or predator-specific predation rates. This analysis does not rely on continuous camera monitoring; therefore, we included observation periods outside of the video-recorded periods given that we could conclude that the nest was still active during routine nest monitoring. We evaluated support for 21 models describing daily nest survival rates that included main effects models of linear date, quadratic date, location, and nest stage along with habitat factors including distance to nearest edge, nest height, and mean percent concealment. We also considered additive effects of location, linear date, and nest stage with the habitat factors. We extrapolated period survival

based on 14 days and 11 days for incubation and nestling stages, respectively (Grzybowski 1995).

We determined support for 11 models of predator-specific nest predation using multinomial logistic regression in an information-theoretic framework (Thompson and Burhans 2003). We pooled data across years because of small sample sizes of predation events within individual years. Models included additive effects of linear date, and nest stage, along with habitat factors including distance to nearest edge, nest height, and mean percent concealment. We were interested in general patterns of predator-specific predation regardless of location, so if location was a significant factor affecting nest success, we planned to control for location effects by including it in all predator-specific models.

For predator-specific predation, our sampling unit was each 24-hour interval during which cameras recorded activity at each nest. If the camera failed to record video during an interval, we removed that interval from analyses unless we were able to confirm that no predation events occurred during that period. We used 5 response categories in our multinomial logistic regression analysis for predator-specific rates. Four categories represented specific predator groups: birds, snakes, ants, and mammals. We grouped these together because predators within each group use similar foraging strategies, regardless of individual species.

We compared the 4 predator categories against another fifth category representing other causes of failure and nests that successfully fledged young. Other causes of failure included abandoned nests, nest losses due to weather events, or nest failure due to unhatched eggs or nestling mortality not caused by predation. We did not include camera-monitored nests that were depredated in this analysis if we could not identify the predator on video or the camera equipment failed to record the predation event.

We ranked models based on their Akaike's Information Criterion (AIC) values and weights (Burnham and Anderson 2002). We considered a model competitive if the $\Delta AIC \leq 2$. We used a likelihood-ratio test to assess goodness-of-fit of the global model. Additionally, we used model averaging and examined coefficients and 95% confidence intervals for significance of effects.

RESULTS

We monitored 115 vireo nests with cameras in 2008 and 2009, including 31 in Coryell County, 41 in Kerr, and 43 in Devils River (Table 1). We located 68% of nests during the early (\leq day 4) incubation stage, resulting in 855 camera-recorded days during incubation, and 557 observation days during the nestling stage. Two vireo nests in Coryell County and 1 nest at Devils River were not parasitized but were later abandoned when the eggs failed to hatch during incubation and 1 nest in Kerr was abandoned because of the presence of a gray fox disturbing, but not depredating the nest. Additionally, 1 nest was lost to weather events. No nests were abandoned as a result of camera placement. Mean time until adults returned to normal behavior after camera deployment was < 7 minutes (M. L. Morrison, Texas A&M University, unpublished data).

Table 1. Nest fates and percentage of nests parasitized by brown-headed cowbirds for camera-monitored black-capped vireo nests at Coryell County, Kerr, and Devils River, Texas in 2008 and 2009.

	Location									
	Coryell County				Kerr				Devils River	
	2008		2009		2008		2009		2009	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Parasitized	25.0	2	43.4	10	10.0	2	23.8	5	37.2	16
Failed	80.0	6	65.2	15	45.0	9	66.7	14	72.1	31
Fledged	20.0	2	30.4	7	50.0	10	33.3	7	27.9	12
Unknown	0.0	0	4.3	1	5.0	1	0.0	0	0.0	0
Total nests		8		23		20		21		43

Habitat measurements by location (Table 2) varied for distance to nearest edge ($F_{2,112} = 18.13, P \leq 0.001$) and concealment ($F_{2,112} = 26.67, P \leq 0.001$), but not for mean nest height ($\bar{x} = 1.22 \pm 0.43$ m; $F_{2,112} = 0.09, P = 0.914$). Distance to nearest edge and minimum patch size had high correlation ($r^2 = 0.81$), thus we only used distance to nearest edge in subsequent analyses. Distance to nearest edge and minimum patch size at Coryell County were approximately 4 times greater than at Kerr and Devils River. Mean vegetation concealment was lowest at Coryell County and highest at Devils River, increasing approximately 10% from Coryell County to Kerr, and 10% from Kerr to Devils River.

Nest Searching and Video Monitoring

In 2008 and 2009, we recorded 39 predation events by ≥ 9 predator species (Table 2). Brown-headed cowbirds were the most frequent predator at nests (31%, $n = 39$). In 92% ($n = 12$) of all recorded cowbird predation events, the adult cowbird did not lay an egg in the nest following removal of the nest contents. At the 1 nest where this occurred, the cowbird removed all 4, 3-day-old vireo nestlings from the

nest, and then laid an egg in the empty nest; we classified this as a predation event. We only camera-monitored nests after the start of incubation (period following laying of the penultimate egg), thus our results did not include a majority of parasitism events that likely resulted in the removal of a host egg, as is commonly documented.

Snakes were responsible for 26% ($n = 39$) of nest predation events, contributing to 38% ($n = 8$) and 30% ($n = 17$) of events in Coryell and Kerr Counties, but were similar in frequency to ant and mammal predation events in Devils River (Table 3). In Coryell County, cowbirds were the only avian predator we observed, whereas both Kerr and Devils River also had multiple predation events by western scrub-jays and roadrunners (*Geococcyx californianus*), respectively.

We documented 17 predation events during the incubation stage and 22 during nestling. The majority of predation events by mammals (3 of 4 events) occurred during incubation, whereas 75% ($n = 12$) of predation events by cowbirds occurred during the nestling stage and most events (83%; $n = 12$) resulted in nest failure. We found no difference in predation events by nest stage for other predator groups.

Table 2. Minimum, maximum, and mean (\pm SE) for habitat variables of black-capped vireos nests in Coryell County, Kerr, and Devils River, Texas in 2008 and 2009.

Habitat variable	Min.	Max.	$\bar{x} \pm$ SE
All locations			
Nest height (m)	0.6	2.7	1.22 \pm 0.04
Distance to edge (m)	0.0	16.0	2.61 \pm 0.36
% concealment	19.9	98.5	75.03 \pm 1.42
Minimum patch size (m ²)	1.1	1,250.0	148.48 \pm 25.1
Coryell County			
Nest height (m)	0.6	2.0	1.25 \pm 0.07
Distance to edge (m)	0.8	25.0	5.76 \pm 1.04
% concealment	19.9	94.9	63.04 \pm 3.09
Minimum patch size (m ²)	14.8	1,250.0	404.47 \pm 71.2
Kerr			
Nest height (m)	0.6	2.7	1.22 \pm 0.70
Distance to edge (m)	0.0	3.3	1.50 \pm 0.14
% concealment	45.1	93.4	73.9 \pm 1.76
Minimum patch size (m ²)	2.8	328.8	40.76 \pm 8.05
Devils River			
Nest height (m)	0.6	2.7	1.21 \pm 0.07
Distance to edge (m)	0.1	16.0	1.40 \pm 0.38
% concealment	58.3	98.5	84.7 \pm 1.47
Minimum patch size (m ²)	1.1	734.7	66.64 \pm 18.9

Table 3. Nest predators recorded removing nest contents (eggs or nestlings) using video cameras at black-capped vireo nests in Coryell County, Kerr, and Devils River study regions in Texas, 2008 and 2009.

Predator	Location		
	Coryell County (<i>n</i>)	Kerr (<i>n</i>)	Devils River (<i>n</i>)
Snake spp.			
<i>Elaphe</i> spp.	3	5	2
Hawk spp.			
<i>Accipiter</i> spp.	0	1	0
Greater roadrunner			
<i>Geococcyx californianus</i>	0	0	2
Western scrub-jay			
<i>Aphelocoma californica</i>	1	3	1
Brown-headed cowbird			
<i>Molothrus ater</i>	3	5	4
Ant spp.	1	2	2
Coyote			
<i>Canis latrans</i>	0	1	0
Gray fox			
<i>Urocyon cinereoargenteus</i>	0	0	2
Ringtail			
<i>Bassaris cusastatus</i>	0	0	1
Total	8	17	14
Unknown predator	3	1	11

Nest Predation Modeling

For nest survival modeling, we used 114 nests (excluding 1 camera-monitored nest whose nest fate was unknown). Daily survival rates were best explained by nest stage; all competitive models with $\Delta\text{AIC} \leq 2$ contained nest stage (total AIC weight = 0.87; Table 4). Nest survival was lower during the nestling stage relative to laying and incubation stages (nestling $\beta = -0.66$, 95% CI = -1.165 to -0.158). Estimated daily nest survival during the laying and incubation stage was 0.985 (95% CI = 0.967–0.993) and 0.944 (95% CI = 0.921–0.961) during the nestling stage, resulting in period survival of 0.809 for laying and incubation stages combined and 0.531 for nestling stage. Because location was not included in the top models, we did not control for location effects in the predator-specific analysis.

For nest predation modeling with multinomial logistic regression, we used 92 of the 115 nests (1,412 observation days), excluding 18 nests without usable footage, 1 nest with an unknown nest fate, and 12 depredated nests where the predator was not identifiable; failure to identify predators was because of camera equipment malfunctions. We recorded 1 weather-related nest failure where wind was likely responsible for removing all eggs from the nest. We documented predation by 2 predators simultaneously at a nest in Kerr at

which a snake was consuming 4-day-old nestlings when a coyote attacked both the snake and nest, pulling them both from the vegetation. For this nest, we assigned a snake predation to the previous 24-hour sampling interval and the coyote to the next 24-hour sampling interval.

We included 2 nests with predation events that were not recorded on video, but were classified as avian predators based on nest remains and the presence of a cowbird egg in 1 nest. Results of the likelihood ratio test for the global model for 4 predator categories was significant ($\chi^2 = 47.388$, $P = 0.012$), indicating that the model fit the data.

Model results indicated that nest height and marginally, nest stage, best explained predator-specific predation rates (Table 5). Daily predation rates by snakes decreased with increasing nest height (Table 6; Fig. 2), but height was not significant for nests depredated by birds, ants, or mammals. Based on the model with nest stage and nest height, nests in the nestling stage were 2.3 times more likely to be depredated by a bird than nests in incubation stage (Table 6). Daily probability of predation based on the multinomial best-fit model that included nest height was 0.015 for nests depredated by birds, 0.004 for snakes, 0.003 for ants, and 0.002 for nests depredated by mammals.

Table 4. Model selection results for logistic-exposure models of daily nest survival for all black-capped vireos nests ($n = 114$) in Coryell, Kerr, and Devils River, Texas in 2008 and 2009.

Model	ΔAIC^a	ω^b	AIC	LL ^c	K^d
Nest stage	0.00	0.26	487.83	−241.91	2
Nest stage + nearest edge	0.49	0.20	488.32	−241.16	3
Nest stage + % concealment	1.55	0.12	489.38	−241.70	3
Nest stage + nest height	1.72	0.11	489.55	−241.77	3
Linear date + nest stage	1.91	0.10	489.74	−241.87	3
Location + nest stage	2.22	0.08	490.05	−241.02	4
Constant survival	4.62	0.03	492.45	−245.22	1

^a Change in Akaike's Information Criterion (AIC) relative to the model with the smallest AIC value.

^b AIC model weight.

^c Log-likelihood.

^d Number of parameters.

Table 5. Model selection results for multinomial logistic-exposure models of effects on predator-specific predation rates of black-capped vireos nests ($n = 92$) in Coryell County, Kerr, and Devils River, Texas in 2008 and 2009.

Model	ΔAIC_c^a	ω^b	AIC_c	LL ^c	K^d
Nest height	0.00	0.31	462.14	−223.02	8
Nest stage + nest height	0.45	0.25	462.58	−219.18	12
Constant survival	1.66	0.14	463.80	−227.88	4
Nest stage	2.17	0.11	464.31	−227.10	8
% concealment	2.74	0.08	464.88	−224.39	8
Nest stage + % concealment	3.13	0.07	465.27	−220.52	12
Linear date	5.90	0.02	468.04	−225.97	8
Nest height + distance to edge	6.07	0.01	468.21	−221.99	12
Distance to edge	7.20	0.01	469.34	−226.62	8
Nest stage + distance to edge	7.82	0.01	469.96	−222.87	12
% concealment + distance to edge	7.98	0.01	470.12	−222.95	12
Location	11.03	0.00	473.17	−222.47	12

^a Change in Akaike's Information Criterion corrected for small sample size (ΔAIC_c) relative to the model with the smallest AIC_c value.

^b AIC_c model weight.

^c Log-likelihood.

^d Number of parameters.

Table 6. Model-averaged parameter estimates, standard error, and 95% confidence intervals for predators classes from top models determined by multinomial logistic-exposure modeling for effects on predator-specific predation rates of black-capped vireos nests in Coryell County, Kerr, and Devils River, Texas in 2008 and 2009.

Parameter	Predator class	Estimate ± SE	95% CI	
Nest height	Birds	0.12 ± 0.52	-0.90	1.14
	Snakes	-2.88 ± 1.19	-5.23	-0.54
	Ants	-1.20 ± 1.32	-3.78	1.38
	Mammals	0.74 ± 1.18	-1.57	3.05
Nest stage	Birds	1.14 ± 0.47	0.23	2.06
	Snakes	0.30 ± 0.61	-0.90	1.49
	Ants	0.88 ± 0.92	-0.91	2.68
	Mammals	-0.23 ± 1.23	-2.63	2.18

DISCUSSION

Vireo nest success remains limited at multiple breeding sites across Texas, but the risk of nest predation depends primarily on habitat characteristics and nest stage, regardless of location. Our results from modeling daily nest survival indicated that nest stage was a major factor determining survival rates across all locations. We expected lower nest survival during the nestling stage, given the major nest predators. Both snakes and avian predators use visual cues to locate potential prey and identify active nests (Clotfelter 1998, Mullin and Cooper 1998, Robinson and Robinson 2001), so increased nest activity associated with feeding nestlings could likely attract predators.

Daily nest survival was similar across locations relative to the other models in this analysis, even with the significant variability we found in vegetation characteristics. Nest height was consistent between locations, indicating vireos may have a preferred range of nest heights regardless of region. However, distance to edge, minimum patch size, and nest

concealment measurements differed between locations. Shorter distances to edge related to smaller vegetation clumps available across the study areas, and nest concealment was influenced by the species of vegetation in each region. This does not explain why vireos in Coryell County nested significantly farther from the habitat edge, unless birds may be selecting nest locations based on the dimensions of the vegetation clump, as opposed to distance from the habitat edge. Vireos breeding farther north could be selecting interior nest locations to create vegetative buffers to reduce predation risk from nest predators specializing in edge habitat mentioned in Sperry et al. (2009). However, we did not find that distance to edge affected predator-specific predation rates; therefore, variation in size of available vegetation patches may be driving the differences in distance to edge among the study sites.

Although rates of nest survival were consistent across locations, the most influential predators may have varied by location. Small sample sizes precluded us from testing predator-specific predation rates among study sites; however, putative predators varied by site and summary statistics revealed differing proportions of predation events by taxa among sites. The percentage of snake predations at Coryell County and Kerr were comparable to previous predation data from Fort Hood (Stake and Cimprich 2003). However, we did not observe this pattern in the Devils River region, where multiple mammalian and avian predators comprised the predator assemblage. The arid, hot environment in southwest Texas may preclude predation by snakes, because snakes restrict foraging activity to nocturnal periods during the summer when temperatures are cooler (Sperry et al. 2010), thus making them less likely to locate nests by visual activity (Mullin and Cooper 1998). Texas ratsnakes do not occur in the Devils River region, but 2 other closely related species, the Trans-Pecos ratsnake (*Bogertophis subocularis*) and Baird's ratsnake (*Elaphe bairdi*), occur in the area and likely share similar foraging patterns. Additionally, we observed the predations by mammals at Devils River occurred solely along riparian corridors, which may facilitate easy access to nests in otherwise dense vegetation (Kuehl and Clark 2002).

We only recorded 8 total predation events in Coryell County, but the lack of recorded mammalian predator events is not surprising given previous research on predator assemblages at Fort Hood (Stake and Cimprich 2003) adjacent to our study areas. On private properties in Texas, landowners often physically remove meso-carnivores because they are believed to be detrimental to livestock and game species. This predator management strategy may explain the lack of recorded events involving these meso-carnivores, although no specific information for predator removals on our study areas was available.

Our results for predator-specific models indicate nest stage significantly influences predation risk by birds; predation rates increased in the nestling stage. This supports our previous prediction that predation risk will be greater during nesting stage because avian predators use increased activity as visual cues to locate nests. It also corroborates with our

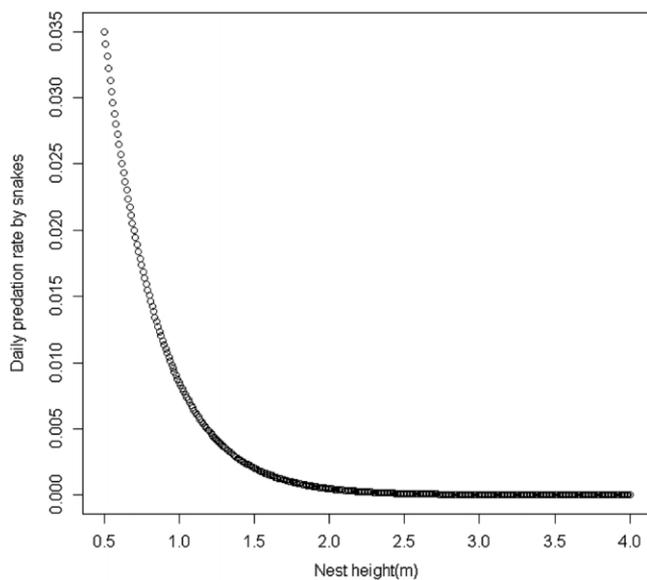


Figure 2. Predicted daily predation rate by nest height by snakes on black-capped vireo nests in Coryell County, Kerr County, and Val Verde County, Texas in 2008 and 2009.

best-fit nest survival model that included nest stage as a major factor because avian species were the most frequent predator at all locations (Table 3).

A surprising observation was the proportion of predation events (31%, $n = 39$) by brown-headed cowbirds, especially during the nestling stage (75%, $n = 12$), and 10 of 12 events resulted in complete nest failure. Predation events by cowbirds at our study sites were greater than previous reports at Fort Hood (15%, $n = 59$ predation events); where 1 of 9 events resulted in complete nest failure (Stake and Cimprich 2003). Predation by cowbirds for other host species also is reportedly lower at 12% ($n = 57$), with cowbirds attempting total nest destruction at 3 of 7 nests (Granfors et al. 2001). Cowbird predation events were recorded in other studies, but the definition of predation event is not consistent in the literature. For example, Benson et al. (2010) reported that cowbirds accounted for 34% ($n = 32$) of predation events of Swainson's warbler (*Limnothlypis swainsonii*) nests, but they included camera-documented parasitism events as nest predations, as opposed to our definition that solely included cowbird predation events where we observed no subsequent laying of a cowbird egg.

Predation of nests by cowbirds on our study locations indicated that these events may be even more common in areas with little or no cowbird trapping, and that the impact of cowbirds on vireos may be much greater than previously believed. Based on the cowbird predation hypothesis (Arcese et al. 1996, Hoover and Robinson 2007), cowbirds are predicted to depredate nonparasitized nests to create future parasitism opportunities. Although we did not directly test this hypothesis, our results provided some anecdotal support for this concept, as every cowbird predation recorded only occurred at nonparasitized nests. However, we did not have a sufficient sample to determine if subsequent vireo nests were more likely to be parasitized by cowbirds. Intensive, widespread cowbird trapping on Fort Hood, which reduced parasitism to <10% from 1997 to 2006 (Kostecke et al. 2005), likely reduced nest predation by cowbirds (Stake and Cavanagh 2001). Even with localized trapping on the majority of our study properties, parasitism rates in Coryell County still averaged 31%. At the other study location with trapping, Kerr had lower parasitism rates than Coryell County (17%, $n = 41$ nests; Table 1), but a greater frequency of cowbird predation.

Land use practices on private or public lands may not be beneficial for endangered species management, especially regarding cowbirds. Both privately owned properties and state-managed lands included in our study managed their property primarily for ranching and hunting purposes. The increased grazing practices of livestock or supplemental feeding of certain animals (e.g., white-tailed deer [*Odocoileus virginianus*]) for hunting on or near all of our study properties may promote increased populations of cowbirds (Goguen and Mathews 2000), thus increasing both the risk of parasitism and predation for vireo nests.

Our predator-specific analysis indicated that nest predation rates by snakes were influenced by nest height. Predation by snakes decreased with increasing nest height, corresponding

to our predictions. Pierce et al. (2008) found that Texas ratsnakes showed a peak of arboreal activity during summer months (as opposed to ground-based foraging), which extends after the peak of avian breeding activity. Additionally, Sperry et al. (2009) noted that Texas ratsnakes often basked in the top of canopies in oak-juniper woodlands, and that golden-cheeked warblers (*Setophaga chriso- paria*) experienced lower nest survival with decreasing nest height. If snakes in Texas are spending the majority of time in an arboreal setting, they may be more likely to detect nests located higher in wooded substrates. As a result, if vireos breed in larger habitat patches with reduced edge, they may still be vulnerable to snake predations, but only if they nest in close proximity to the vegetative canopy because the canopy could also function as a habitat edge.

MANAGEMENT IMPLICATIONS

Although rates of nest survival were consistent across locations, the most influential predators may have varied by location, suggesting localized recovery strategies for the vireo may benefit future recovery efforts of the species. However, 4 predators occurred in all regions, and 2 major predators (snakes and brown-headed cowbirds) were among the most common to all regions.

The risk of nest depredation by snakes appeared to decrease with increasing nest height. Effectively managing vireo habitat to maximize patch size may reduce vireo risk to snakes, especially if snakes frequently use edge or arboreal habitat. Regarding other identified nest predators, fire ant impact on vireo nests may be less influential than previously believed, despite their widespread occurrence. However, avian predators, especially brown-headed cowbirds, may have a greater impact than previously believed on nest survival of black-capped vireos, negatively affecting nest survival through both parasitism and frequent predation of nonparasitized nests. Land management strategies should include examining methods to reduce the risk of cowbird parasitism or predation. Additionally, our results indicated that cowbird predation of vireo nests may create future parasitism opportunities; further research may be needed to understand the consequences of cowbird nest predation and to determine effective management strategies for the species.

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