Factors Affecting Nest Success and Predator Assemblage of Breeding Birds in Semiarid Grasslands☆

Helen T. Davis [a],*, Ashley M. Long [b,1], Jeremy A. Baumgardt [b], Tyler A. Campbell [c], Michael L. Morrison [a]

[a] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA
[b] Texas A&M Natural Resources Institute, College Station, TX 77843, USA
[c] East Foundation, San Antonio, TX 78216, USA

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ABSTRACT

Woody encroachment has influenced wildlife distributions and, thus, predator-prey dynamics, for many taxa in North American grasslands. In 2015 and 2016, we examined how vegetative characteristics influenced avian nest predator assemblages and nest predation rates in semiarid grasslands of south Texas, where encroachment of woody plant species is common. We monitored 253 nests of 17 bird species and deployed infrared cameras at 107 nest sites within four vegetation types at our study sites. We also used data from a concurrent, multispecies monitoring project within our study area to assess predator activity within these same vegetation types. We divided bird species into four nest types based on nest shape and size (i.e., small, medium, and large cup-shaped nests and exposed nests with little structure). We then used logistic regression to examine relationships between shrub cover, concealment, and distance to edge and the probability of nest success and predation by snakes. We observed a significant decrease in nest success of our medium-sized, cup-shaped nest type when shrub cover increased at the nest site, indicating small increases in shrub cover ($\approx$10%) could have substantial impacts on birds using this nest type. Snakes were our primary predator at camera-monitored nests (59%), and snake activity increased by 6.7% with every 10% increase in shrub cover at the nest site. Mesomammalian and large mammalian predators were most active in vegetation types predominated by herbaceous cover, small mammals were most active in vegetation types predominated by woody cover, and snake activity was highly variable. Predator activity did not reflect predator identity at camera-monitored nests, suggesting that potential nest predator activity may not accurately reflect the risk of nest predation. Results of our study will help inform management of bird species using semiarid grasslands affected by woody encroachment and offer recommendations for improved nest success.

Introduction

Over the past 150–200 yr, agricultural industrialization and urban development have caused widespread loss, fragmentation, and degradation of native grassland and concurrent loss of grassland-dependent wildlife in North America (Samson and Knopf, 1994; Noss et al., 1995; Conner et al., 2001; Brennan and Kuvlesky, 2005). Population declines associated with alterations of grassland habitat are particularly well documented for birds (Pietz and Granfors, 2000; Brennan and Kuvlesky, 2005; Stanley, 2010). Woody encroachment in remaining grasslands,

which has occurred due to intensive grazing, fire suppression, and fluctuating levels of atmospheric carbon dioxide (Archer et al., 1995), has been especially problematic for birds that nest in these systems. Increased shrub cover can alter structure and composition of vegetation available for breeding (Greenfield et al., 2002), opportunities for nest concealment (Davis, 2005), and increase exposure to edge (Lahti, 2001; Batary and Baldi, 2003), which, in turn, may alter predator assemblages, densities, and activity (Blouin-Demers and Weatherhead, 2001; Liebezeit and George, 2002; Thompson and Burhans, 2003; Klug et al., 2010). Because predation is the primary cause of nesting failure in birds (Martin, 1993; Thompson, 2007), a better understanding of how woody vegetation influences avian nest success, nest predator assemblages, and nest predator activity in grasslands could provide insight into predator-prey dynamics and help inform land management actions aimed to improve conservation of grassland nesting birds.

In the southern United States, where encroachment of woody plant species such as honey mesquite (*Prosopis glandulosa* Torr.) is extensive

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(Archer et al., 1995; Van Auken, 2009) and has transformed savannas into subtropical thornscrubs (McMahan et al., 1984; McLendon, 1991), predators of bird nests are mammals such as coyotes *(Canis latrans)*, spotted skunks *(Spilogale* spp.), striped skunks *(Mephitis mephitis)*, American badgers *(Taxidea taxus)*, and bobcats *(Lynx rufus)*; snakes such as rat snakes *(Pantherophis* spp.), whipsnakes *(Masticophis* spp.), and bullsnakes *(Pituophis catenifer sayi)*; and avian species such as brown-headed cowbirds *(Molothrus ater)*, corvids *(Corvus* spp.), and hawks *(Accipiter* spp.; Folse and Arnold, 1978; Robinson et al., 1995; Hernandez et al., 1997; Stake and Cavanagh, 2001; Conkling et al., 2012; DeGregorio et al., 2014; Locatelli et al., 2016). The relative contribution of each potential nest predator to overall nesting success of grassland birds varies widely across geographic locations, ecological conditions, and bird species of interest. For example, coyotes and American badgers accounted for almost 50% of northern bobwhite *(Colinus virginianus)* nest predations in a south Texas study (Rader et al., 2006). Alternatively, a study of black-capped vireos *(Vireo atricapilla)* in central Texas indicated that coyotes and other mesomammalian and large mammalian predators (predators with mid and top trophic level rankings) accounted for a smaller percentage of nest predations compared with snake and avian predators (Conkling et al., 2012). On the basis of research conducted outside of Texas, birds nesting close to forest edges and shrubby patches in grassland ecosystems were particularly vulnerable to nest predation by snakes (DeGregorio et al., 2014) and those grassland birds that had large spatial overlap with snakes had lower nest success than those grassland birds that did not exhibit the same distributional overlap with these potential nest predators (Klug et al., 2010).

Using field observations and camera data collected in 2015 and 2016, we examined how vegetative characteristics influenced nest success, avian nest predator assemblages, and avian nest predator activity at two spatial scales in semiarid grasslands of south Texas. Our specific objectives were to 1) evaluate the influence of woody encroachment on bird nest success at the nest-site scale across a continuum of vegetation types in a region historically dominated by semiarid grasslands; 2) identify avian nest predators across these same vegetation types; 3) evaluate the influence of nest-site vegetation characteristics on the probability of predation by small, mid, and large mammalian, snake, and avian nest predator types; and 4) examine relationships among predator activity, nest success, and predator assemblage across these same vegetation types. Relationships among nest success, predation, and predator assemblage are complex; however, understanding how vegetative characteristics drive these factors at multiple spatial scales could help land managers predict the effects of woody encroachment and help inform subsequent management actions aimed to improve conservation of grassland nesting birds.

We hypothesized that avian nest success would vary on the basis of the type of nest they constructed (detailed later), that the probability of nest success for all birds would increase with increased vegetative concealment of the nest site, and that nest success of all birds would decrease with increased distance from the nest to the nearest edge (i.e., transition from one vegetation type to another). We also hypothesized that we would observe more nest depredation events by mesomammals and large mammals and birds in vegetation types dominated by grasses than vegetation types dominated by woody plants because these types of potential nest predators rely on visual cues to find prey (Whelan et al., 1994). Alternatively, we hypothesized that we would observe more nest depredation events by small mammals and snakes in vegetation types dominated by woody plants because these predators rely on woody cover for protection and thermoregulation (Blouin-Demers and Weatherhead, 2001; Stanley, 2010). We hypothesized that the probability of nest predation by mesomammalian and large mammalian and avian predators would decrease with increased shrub cover at the nest site and that the probability of nest predation by snake and small mammalian predators would increase with increased shrub cover at the nest site. Finally, we hypothesized that

mesomammalian and large mammalian activity and avian activity would increase in vegetation types dominated by grasses, rather than woody plants, and small mammal activity and snake activity would increase in vegetation types dominated by woody plants.

Methods

Study Area

We conducted our research on the East Foundation's approximately 61 000-ha San Antonio Viejo Ranch (SAVR) located in Jim Hogg and Starr Counties, 25 km south of Hebbronville, south Texas (lat: 26.956671, long: −98.835408; Fig. 1). In addition to supporting field laboratory activities, SAVR is managed as a working cow-calf operation. Mean annual temperature in this region is 22°C with annual ranges between 7°C and 36°C. Mean annual rainfall in this region is 50.3 cm (PRISM Climate Group, 2017). Mean temperature during the avian breeding season (March–August) was 25.7°C in 2015 and 27.2°C in 2016 (PRISM Climate Group, 2017). Mean rainfall during the avian breeding season was 14.1 cm in 2015 and 13.0 cm in 2016 (PRISM Climate Group, 2017).

We searched for nests across approximately 35 000 ha at SAVR in four vegetation types as defined by McLendon et al. (2013): early seral, native grassland, shrubland (dominated by woody plants < 3 m tall), and woodland (dominated by woody plants > 3 m tall). Early seral vegetation occurred on < 10% of our study area and is characterized by doveweed *(Croton* spp.), sandbur *(Cenchrus* spp.), and horsemint *(Monarda punctata* L.). Native grassland occurred on < 10% of our study area and included species such as arrowfeather threeawn *(Aristida purpurascens* Poir.), balsamscale grass *(Elyonurus tripsacoides* Humb. & Bonpl. ex Willd.), and seacoast bluestem *(Andropogon littoralis* Nash.). Shrubland occurred on < 10% of our study area and included catclaw *(Acacia greggii* Gray.), blackbrush *(Acacia rigidula* Benth.), and brasil *(Condalia hookeri* M.C. Johnst). Finally, woodland occurred on approximately 70% of our study area and consists primarily of honey mesquite *(Prosopis glandulosa* Torr.) and woody species such as amargosa *(Castela texana* Torr & Gray.) and whitebrush *(Aloysia lycioides* Cham.).

Nest Success

We randomly established two 600-m^2 grids within each of the vegetation types to serve as our study sites. We determined grid size on the basis of nesting density of birds in this region (Flanders et al., 2006), size and shape of vegetation types, and logistics necessary for travel between study sites. We systematically searched for nests across each study site every 3–5 d between 15 March and 15 August of 2015 and 2016. Each yr we provided 2 d of training for two to three technicians on nest searching and monitoring techniques. In early seral and grassland vegetation, we walked 200-m transects spaced 10 m apart while using a bamboo pole to agitate grass and flush birds (Winter et al., 2003). In shrubland and woodland vegetation types, we used behavioral cues, as well as systematic searching, to locate bird nests. We also found nests opportunistically during routine checks of other nests and while traveling between study sites. Once we located a nest, we recorded the number of eggs or nestlings, if present. We placed a small flag marker approximately 10 m from the nest in a random cardinal direction to aid in relocation of the nest site during subsequent visits. We monitored nests every 2–4 d to determine nest success or failure. We determined success or failure by evaluating cues at or in close proximity to the nest (e.g., disturbance, presence of fecal sacs, presence of fledglings, timing within nesting cycle). We did not walk directly to a nest or from the same direction during a nest check so as not to alert potential predators of the nest location. If any predators were visible, we did not check the nest and returned after 1–2 h. We made no effort to mask our scent, as previous studies in both grasslands and forests
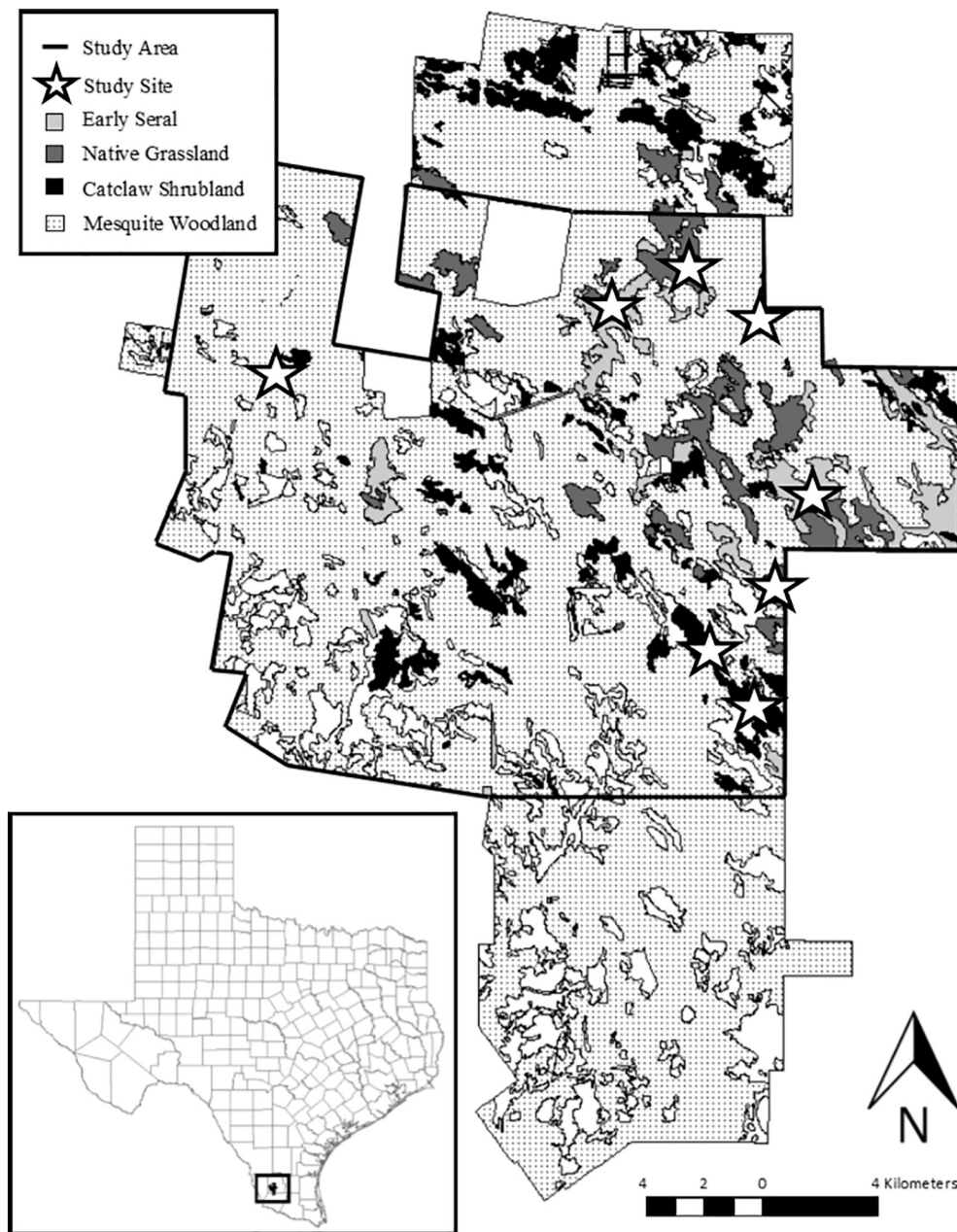
Figure 1. Location of study area and study sites for nest predation study and distribution of vegetation types on San Antonio Viejo Ranch, Texas.

indicated no increase in the probability of predation rates associated with olfactory cues left by observers (Kirkpatrick and Conway, 2010; Jacobson et al., 2011).

　　We conducted vegetation surveys at each nest site within 2 wk of successful fledging of young or nest failure. We used a modified version of BBIRD protocol (Martin et al., 1997) to quantify percent shrub cover in close proximity to the nest site, nest concealment, and distance from the nest site to the closest vegetation or anthropogenic edge. We defined edge as any feature that could drive movement or foraging activity of the potential predator species described earlier and included the distinct boundary between two vegetation types (e.g., distinct forest boundaries or as described by McLendon et al., 2013). Before conducting vegetation surveys, we provided 8 h of training for technicians on estimation techniques and performed surveys together bimonthly to recalibrate estimations and ensure accuracy and consistency across surveyors. We established a 5-m radius circle around each nest site and divided the circle into four quadrants on the basis of four cardinal

directions. Within each quadrant, we visually estimated the percent shrub cover (i.e., woody perennials < 2 m tall covering the ground) to the nearest 10%. We calculated mean percent shrub cover at each nest site as the sum of all percent shrub cover estimates divided by four. We estimated concealment (i.e., percent of nest obscured by vegetation) from 1 m away in each cardinal direction, above and below the nest (Burhans and Thompson, 1998), to the nearest 10%, then calculated the mean of these six values. We estimated distance to edge to the closest 1 m using ArcMap 10.2 (ESRI, 2011, Redlands, CA) and visually in the field.

Nest Predator Observations

　　On a subset of nests, we placed infrared video cameras approximately 30 cm from the nest site or close enough to view contents and activity around the nest without causing unnecessary disturbance to the birds (Pietz et al., 2012). We selected nests on the basis of logistics

(distribution and accessibility across the ranch), availability of camera units, and nest placement (nests placed > 2.5 m high in the canopy could not be monitored with cameras without disturbing the birds). We used video camera systems that consisted of an infrared camera (Rainbow, Costa Mesa, CA), digital video recorder (DVR, Detection Dynamics, Austin, TX), 12-volt battery, and supplemental 20-watt solar panel (Suntech, San Francisco, CA). We used weatherproof 3.6-mm black and white bullet cameras with 940-nm infrared light-emitting diodes. We connected the DVRs to our cameras using a 15-m component cable. We used 32-GB memory cards to increase data storage and decrease the need for nest visitation to change cards on DVRs. We checked camera systems every 2–4 d to change memory cards and repair equipment, if necessary. We only placed cameras at nests with contents (eggs or nestlings) to avoid nest abandonment by adult birds. After installation, we covered cables with ground litter to make cameras less conspicuous to predators. We reviewed video footage using a portable viewfinder at the next check to confirm that adults were attending the nest.

We reviewed camera footage until we confirmed an initial nest predation event. We did not use subsequent predators of specific nests in this study since previous studies indicate that initial predation rates are the most effective measure of predation risk (Pietz and Granfors, 2000). If continuous camera footage was interrupted due to failed/damaged equipment, weather, or skewed/blocked camera visuals, we confirmed all nest contents were remaining when footage resumed. If contents were missing, we identified the predator as unknown and did not include these events in predator-specific analyses. We then grouped predators into one of five categories on the basis of taxonomic class: mesomammal/large mammal, small mammal, snake, bird, ant (*Solenopsis* spp.), or cow *(Bos taurus x indicus)*/deer *(Odocoileus virginianus).*

We measured mesomammal and large mammal activity using track plates. We constructed transects using four track stations, spaced 250 m apart, and conducted sampling efforts between 15 March and 15 August of 2015 and 2016. We randomly selected the location and orientation $(0-359°)$ of each transect within each vegetation type; however, transect orientation was limited due to shape and size of vegetation patches. Most commercial baits are only effective to 200 m; thus, we did not monitor nests that were located within 250 m to a track plate to avoid the influence of baiting on nest success (Peterson et al., 2004). We deployed track plates when nest monitoring began and removed plates once monitoring ended (March through August).

Track stations consisted of one 160 cm × 82 cm aluminum plate. We coated each plate with a 3:1 mixture of isopropyl alcohol and carpenter chalk (Irwin Tools, Martinsville, OH). Once the alcohol evaporated, a thick, uniform layer of chalk remained. We then placed white contact paper sticky side up in the middle of each track plate (Cain, 2001) and lured each track plate with a commercial predator attractant that we selected on the basis of potential predators within our study area (Caven's Predator Bait Plus, Minnesota Trapline, Pennock, MN). We opened stations for approximately 7 days; however, we closed stations if rain was forecasted. During checks we removed contact paper and bait from the station. We then left the unlured stations closed for 7–10 d to discourage predators from becoming acclimated to the bait. After the closure period, we relured track plates and replaced chalk and contact paper.

To account for small mammal activity in our study area, we used data collected by a concurrent monitoring project that involved a substantial sampling effort with the purpose of calculating detection probabilities of species. We sampled small mammal activity between 25 January and 15 April in both 2015 and 2016. We selected sampling dates to coincide with peak activity and to avoid mortality due to heat stress that would result from sampling later in the season. In 2015, we configured Sherman traps (7.6 × 9.5 × 30.5 cm, model XLK) in a 12 × 12 square grid with 20 m spacing at 50% of sampling locations. For larger rodents such as rats, we also placed extralarge Sherman traps (10.2 × 11.4 × 38 cm, model XLF15) at every other station, resulting in a 6 × 6 configuration with 40-m spacing. At the other half of the sites we used a rectangular configuration consisting of three transects. We

constructed transects 300 m in length, with 25 m spacing between Sherman traps (7.6 × 9.5 × 30.5 cm, model XLK) and 25 m spacing between transects, resulting in a 3 × 15 configuration. We also placed extralarge traps (10.2 × 11.4 × 38 cm, model XLF15) every 50 m along the 2 outer transects. In 2016, we also used two trapping configurations. We used an 11 × 11 configuration with 20 m spacing and placed additional extralarge traps at every other location, resulting in a 6 × 6 configuration. At the other half of the sites, we used a 19 × 3 configuration and placed an additional 14 extralarge traps along the outer two lines. Beginning the afternoon before the first trap night, we opened and baited traps and then checked and closed them each morning. We trapped at each site for 6 consecutive nights.

We also used data collected during a concurrent study to determine snake activity. We used a stratified random sampling technique (Morrison et al., 2008:146–148), to determine the location of each sampling location within each vegetation type. We sampled for snake activity between 19 April through 14 August in 2015 and 18 April through 6 August in 2016 to coincide with peak snake activity. We used trap arrays consisting of pitfall traps, funnel traps, and cover boards with drift fencing to sample the diversity of snakes occurring on the ranch. We first used silt fencing and wooden stakes to construct three arms radiating 15 m from a central point. We placed pitfall traps (5-gallon buckets) at the center of the array and at the distal end of each arm. In addition, we placed wire-mesh funnel traps on both sides of the drift fence, approximately 7.5 m from the central pitfall trap on all three arms. We provided each pitfall and funnel trap with a plywood cover board for shade and spaced the cover boards over pitfall traps approximately 3 cm from the ground level with sticks or rocks. We also placed a 61 cm × 122 cm sheet of plywood within 5 m of each of the three distal pitfall traps that acted as cover boards for detecting snakes that are primarily fossorial. To avoid trapping effects on nest success, we did not place bird study grids closer than 50 m to snake trapping locations to account for disruption of natural predator movement around trapping arrays. We trapped each snake array for 30 consecutive nights.

We did not sample for avian predators.

Analyses

Nest Success

We divided the bird species into categories on the basis of the species' nest type. Because differences in nest type could potentially mask relationships between nest success and vegetative characteristics, we used five criteria to categorize nests: nest size, nest shape, nest location (e.g., ground, shrub, or tree placement), incubation time, and nestling time (time nestlings spend in the nest before fledging). We evaluated nest size qualitatively by grouping nests with distinctly different sizes based on their circumference (small = 200 mm, medium = 300 mm, large = 750 mm). We evaluated nest shape by grouping nests into two categories: cup-shaped nests and minimalist nests with little or no structure (hereafter "exposed"). We then evaluated nest location, incubation, and nestling time using life history traits described in Baicich and Harrison (2005). After considering these five criteria, we arrived at four nest types: small-cup nests, medium-cup nests, large-cup nests, and exposed nests.

We developed a priori models to evaluate the effects of vegetation variables on nest success of each nest type. Prior to model evaluation, we checked for statistically significant correlations between variables using variance inflation factors (VIFs). We considered VIF values > 5 to be significantly correlated (O'Brien, 2007). We used a logistic regression approach (Hosmer and Lemeshow, 1989) in R 3.3.2 (R Core Team, 2017) to evaluate the effects of shrub cover, concealment, distance to edge, and presence of camera on nest success (0 = fail, 1 = success) of each nest type. We also included year and Julian date to account for yearly and seasonal variation. We used nest success rather than daily nest survival because both Mayfield (Mayfield, 1961, 1975) and logistic exposure (Shaffer, 2004) methods are rarely used for multispecies

analyses and using nest success allowed us to make more direct comparisons among nest success, probability of predation, and nest-site specific vegetative characteristics. We also included multiple effects models and interaction models using these variables. We evaluated model fit using Akaike's information criterion adjusted for small sample sizes (AIC$_c$) and AIC$_c$ weights (w_i; Sugiura, 1978; Burnham and Anderson, 2002). We considered models with $\triangle$AIC$_c$ values < 2.0 to have similar support. We then selected our highest-ranked model and plotted predicted values and 95% confidence intervals using R 3.3.2 (R Core Team, 2017).

Nest Predator Observations

After evaluating camera footage, we grouped predator species by predator type (e.g., mesomammal and large mammal, small mammal, snake, avian) and constructed frequency tables of detections of individual species between years and within each vegetation type. We then made comparisons of detection frequencies between predator type, year, and vegetation type.

We developed a priori models to evaluate the effect of shrub cover, concealment, and distance to edge on the probability of predation by each predator type detected on camera; however, due to low sample sizes, we could only construct models to evaluate the probability of snake predation on bird nests. We used logistic regression (Hosmer and Lemeshow, 1989) in R 3.3.2 (R Core Team, 2017) and included fixed effects, additive effects, and interaction models using our selected variables. We evaluated model fit using AIC$_c$ and AIC$_c$ weights (w_i; Sugiura, 1978; Burnham and Anderson, 2002:49–97). We considered models with $\triangle$AIC$_c$ values < 2.0 to have similar support. We then selected our highest-ranked model and plotted predicted values and 95% confidence intervals using R 3.3.2 (R Core Team, 2017).

We constructed indices of predator activity for mesomammal and large mammal, small mammal, and snake sampling efforts using captures or detections per trap or station night. Before constructing indices, we selected species within each predator type that are known to depredate or could potentially depredate bird nests based on life history strategies (Schmidley, 1994; Werler and Dixon, 2000). For mesomammal and large mammal sampling, we constructed an index of activity for each species as individual detections of each species per track station per day. Because we could not differentiate between individual prints of the same species on track plates, we counted multiple prints of a single species on an individual plate as one detection for that species within each sampling period. For small mammals, we constructed

activity indices as trapped individuals of each species per trap night. Because we used data from two trapping configurations (rectangular and square), we multiplied values collected at rectangular configurations by 3.75 to correct for differences in trap numbers. For snakes, we constructed activity indices as trapped individuals per trap night. We then multiplied all activity indices by 100 to standardize to 100 trap nights.

Next, we performed statistical tests to evaluate the effects of vegetation type on predator activity indices calculated earlier. We assessed normality and homogeneity of variance of each vegetation type for each predator species using Kolmogorov–Smirnov tests and visually with scatterplots. Because our data violated the assumption of normality, we proceeded with statistical evaluation using nonparametric Kruskal-Wallis tests. We used Kruskal-Wallis tests to test for statistical differences in mean values of activity between each vegetation type for all predator species. We then reported these mean values and associated standard errors and plotted these values using R 3.3.2 (R Core Team, 2017). We then compared results with nest predation frequencies calculated previously.

Results

Nest Success

We monitored 253 nests of 17 bird species in 2015 and 2016 (Table 1). We observed the lowest percentage of apparent nest success in small- and medium-cup types, with 21.3% and 25.3% of nests fledging at least one young, respectively. Large-cup nests (31.3% success) we monitored were 1.2 times more successful than small- and medium-cup nests. We observed the highest success in our exposed nest type (47.7%), which was over two times more successful than small-cup nests. We observed higher nest success in 2015 (small = 27.2%, medium = 26.0%, exposed = 61.5%) when compared with 2016 (small = 16.0%, medium = 24.6%, exposed = 27.8%) for all nesting types except for large-cup nests (2015 = 25%; 2016 = 37.5%).

Our best-fit model for small cup nests was the null model (Table 2). Thus, our a priori variables did not explain success for this type. For medium-cup nests, we observed similar support for our top two models including Julian date ($\beta = 0.02$) and shrub cover ($\beta = -0.06$; see Table 2). For our Julian date model, we observed a 10% increase in predicted probability of nest success for medium cup nests with every increase of 50 Julian d. For our shrub cover model, we observed a 6.3% decrease in predicted probability of nest success for medium-cup

Table 1
Common name, scientific name, and nest type of 17 nesting bird species monitored using visual observation and nest cameras within early seral (ES), native grassland (NG), catclaw shrubland (CC), and mesquite woodland (MW) vegetation types on San Antonio Viejo Ranch, Texas, 2015–2016.

Common name	Scientific name	Nest type	Total monitored				Camera monitored			
			ES	NG	CC	MW	ES	NG	CC	MW
Bewick's wren	*Thryomanes bewickii*	Small cup	1	0	0	0	1	0	0	0
Black-throated sparrow	*Amphispiza bilineata*	Small cup	1	0	7	8	1	0	5	5
Cassin's sparrow	*Aimophila cassinii*	Small cup	6	0	0	2	6	0	0	2
Lark sparrow	*Chondestes grammacus*	Small cup	4	2	0	3	3	2	0	2
Painted bunting	*Passerina ciris*	Small cup	4	2	3	4	2	2	2	2
Cardinal	*Cardinalis* spp.	Medium cup	1	0	0	3	1	0	0	0
Curve-billed thrasher	*Toxostoma curvirostre*	Medium cup	16	0	1	9	6	0	1	3
Eastern meadowlark	*Sturnella magna*	Medium cup	1	0	0	0	1	0	0	0
Green jay	*Cyanocorax yncas*	Medium cup	0	0	0	1	0	0	0	0
Long-billed thrasher	*Toxostoma longirostre*	Medium cup	0	0	0	1	0	0	0	1
Northern cardinal	*Cardinalis cardinalis*	Medium cup	8	1	4	11	1	0	1	2
Northern mockingbird	*Mimus polyglottos*	Medium cup	12	3	4	20	3	0	1	8
Pyrrhuloxia	*Cardinalis sinuatus*	Medium cup	5	4	4	11	2	1	0	4
Scissor-tailed flycatcher	*Tyrannus forficatus*	Medium cup	10	7	1	5	1	0	0	0
Unknown		Medium cup	0	0	0	3	0	0	0	1
Greater roadrunner	*Geococcyx californianus*	Large cup	0	2	3	10	0	2	2	10
Yellow-billed cuckoo	*Coccyzus americanus*	Large cup	0	0	0	1	0	0	0	1
Common ground-dove	*Columbina passerine*	Exposed	5	4	1	5	1	3	0	4
Mourning dove	*Zenaida macroura*	Exposed	14	8	1	6	7	3	0	1
Total			88	33	29	103	36	13	12	46

Table 2
Model selection results from regression analysis of nest success and vegetation variables for three nest types monitored in four vegetation types on San Antonio Viejo Ranch, Texas, 2015–2016.

Nest type[1]	Model[2]	K[3]	LL[4]	AIC$_c$[5]	ΔAIC$_c$[6]	w_i[7]
Small cup						
	Null	1	−24.08	50.61	0.00	0.36
	Yr	2	−23.56	52.61	2.00	0.13
	Shrub	2	−23.69	52.88	2.27	0.12
	Julian	2	−23.82	53.14	2.53	0.10
	Camera	2	−23.96	53.41	2.80	0.09
	Concealment	2	−24.01	53.52	2.90	0.08
	Edge	2	−24.02	53.55	2.93	0.08
	Shrub + concealment	3	−23.39	56.20	5.59	0.02
	Shrub + edge	3	−23.68	56.79	6.18	0.02
	Shrub ● concealment	4	−23.16	60.98	10.37	0.00
	Global	7	−22.29	95.91	45.30	0.00
Medium cup						
	Julian	2	−78.62	162.44	0.00	0.35
	Shrub	2	−78.90	163.00	0.56	0.27
	Shrub + edge	3	−77.44	163.54	1.10	0.20
	Shrub + concealment	3	−78.71	166.09	3.66	0.06
	Camera	3	−79.26	167.18	4.75	0.03
	Null	1	−82.65	167.66	5.22	0.03
	Edge	2	−81.37	167.93	5.49	0.02
	Concealment	2	−81.84	168.87	6.43	0.01
	Shrub ● edge	4	−78.64	170.29	7.85	0.01
	Shrub ● concealment	4	−78.64	170.29	7.85	0.01
	Yr	2	−82.63	170.46	8.02	0.01
	Global	8	−70.06	192.13	29.69	0.00
Exposed						
	Yr	2	−27.96	61.63	0.00	0.44
	Null	1	−30.45	63.41	1.77	0.18
	Edge	2	−28.99	63.70	2.07	0.15
	Camera	2	−29.65	65.02	3.39	0.08
	Shrub	2	−30.19	66.09	4.46	0.05
	Julian	2	−30.20	66.12	4.49	0.05
	Concealment	2	−30.43	66.58	4.95	0.04
	Concealment + edge	3	−28.91	67.82	6.19	0.02
	Concealment ● edge	4	−28.90	73.80	12.17	0.00
	Global	7	−25.73	121.46	59.83	0.00

[1] Nest type as determined by nest size, shape, location, incubation, and nestling time.
[2] Explanatory variable abbreviations: Null indicates null model; Shrub, percent shrub cover at nest site; Concealment, percent of nest obscured by vegetation; Edge, distance to closest edge in meters; Yr, year sampled; Julian, Julian date; Camera, camera-monitored nest; Global, all variables included.
[3] Total parameters in model.
[4] Log likelihood.
[5] Akaike's information criteria corrected for small sample sizes.
[6] AICc relative to the best-fit model.
[7] Model weight.

Table 3
Frequency of fledging events and detection of nest predators identified from initial predation events recorded on nest cameras deployed in early seral (ES), native grassland (NG), catclaw shrubland (CC), and mesquite woodland (MW) vegetation on San Antonio Viejo Ranch, Texas, 2015–2016.

Common name	Scientific name	Predator type	ES	NG	CC	MW
Great Plains rat snake	*Pantherophis emoryi*	Snake	4	0	3	9
Coachwhip	*Masticophis flagellum*	Snake	3	1	0	3
Unknown snake		Snake	1	1	1	3
Unknown mammal		Small mammal	0	0	0	1
Coyote	*Canis latrans*	Meso-/large mammal	1	1	1	2
American badger	*Taxidea taxus*	Meso-/large mammal	0	1	0	0
Chihuahuan raven	*Corvus cryptoleucus*	Avian	1	0	2	1
Brown-headed cowbird	*Molothrus ater*	Avian	0	0	0	1
Cooper's hawk	*Accipiter cooperii*	Avian	1	0	0	0
Greater roadrunner	*Geococcyx californianus*	Avian	0	0	0	1
Northern mockingbird	*Mimus polyglottos*	Avian	1	0	0	0
Eastern screech owl	*Megascops asio*	Avian	1	0	0	0
Ant spp.	*Solenopsis* spp.	Ant	0	1	0	1
Cow	*Bos taurus x indicus*	Cow/deer	0	0	0	1
White-tailed deer	*Odocoileus virginianus*	Cow/deer	1	0	0	0
Total			14	5	7	23
Unknown			0	1	0	0
Weather			1	0	0	0
Predation not recorded			3	1	0	5
Fledged			10	3	0	9

nests with every 10% increase in shrub cover; however, our confidence for predicting nest success with shrub cover > 20% was low due to limited observations above this value. For exposed nests, we found similar support for our year and null models (see Table 2). For our year model (β = −1.43), nest success was 33.7% lower in 2016 than in 2015 for this nest type.

Nest Predator Observations

We deployed infrared cameras at 107 nests and successfully recorded 72 nest fate events that we used for further analysis. Of these fate events, we recorded a total of 22 fledging events, 49 predation events by 12 species, and 1 failure due to weather. Snakes were the most frequent nest predators we detected on camera (n = 29; Table 3). We detected Great Plains rat snakes (*Pantherophis emoryi*) at 32.6% of predation events and coachwhips (*Masticophis flagellum*) at 14.2% of predation events. We detected avian predators (n = 9) at 18.4% of predation events and mesomammals (n = 6) at 12.2% of predation events. We also observed highest species richness in our avian predator type with six bird species detected. Within our mesomammal and large-mammal predator type, we only detected coyotes and badgers. We only observed one nest depredated by an unknown small mammal and two nests depredated by ants. We also observed two nests depredated by large grazing/browsing species, such as cow and deer; however, the cow was observed destroying the nest but did not consume eggs or nestlings.

We observed snakes depredating nests most frequently in woodlands, accounting for > 50% of all predation events in this vegetation type (see Table 3). We observed mesomammals and large mammals depredating more nests in woodlands (n = 2) and grasslands (n = 2) than in early seral vegetation (n = 1) and shrublands (n = 1); however, this difference was negligible. Avian, small mammal, ant, and grazing/browsing predators we observed were variable across all vegetation types.

Due to sample size limitations, we only constructed predation probability models to evaluate the effects of shrub cover, concealment, and distance to edge on the probability of nest predation by snakes. We also included year and Julian date to account for temporal variability. Our best fit model to predict the probability of snake predation included shrub cover (β = 0.07; Table 4). We detected a 6.7% increase in predicted probability of snake predation with every 10% increase in shrub cover, before reaching asymptote around 50% shrub cover, similar to the asymptote for our medium-cup nest type (Fig. 2). However, our confidence for predicting snake predation probability with shrub cover > 20% was low due to limited observations above this value.

We sampled for mesomammal and large mammals for a total of 1 454 track station d in 2015 and 1 421 station d in 2016. In early seral vegetation, we detected higher activity of coyotes and foxes (*Vulpes vulpes, Urocyon cinereoargenteus*) in relation to other potential predators in 2015 and higher activity of coyotes in relation to other potential predators in 2016. We also observed coyotes depredating the most camera monitored nests in comparison with other mesomammal and large mammals. In grasslands, coyotes (2015: x̄ = 1.29, SE = 0.63; 2016: x̄ = 2.45, SE = 1.16) were two times more active than foxes and 4.6 times more active than raccoons (*Procyon lotor*) in 2015, yet these differences were not significant ($x^2 = 2$, $P = 0.37$, df = 2; Fig. 3). Coyotes were the only mesomammal and large mammal predators detected in grasslands in 2016. In shrublands, however, detections of all predators we observed were low in both yr (see Fig. 3). Lastly, in woodlands we observed coyotes (2015: x̄ = 0.072, SE = 0.41; 2016: x̄ = 1.56, SE = 0.65) as the most active predator and were 2.6 times more active than raccoons in 2016; however, this difference was not significant ($x^2 = 1$, $P = 0.32$, df = 1; see Fig. 3). Despite having the lowest activity per predator species, we detected the highest species richness in woodlands in comparison with other vegetation types, similar to predator richness seen on nest cameras.

We sampled for small mammals for a total of 19 980 trap nights in 2015 and 14 532 nights in 2016. In 2015, we observed substantially higher Southern Plains woodrat (*Neotoma micropus*) activity in early seral (x̄ = 0.91, SE = 0.87) and woodland (x̄ = 0.93, SE = 0.26) vegetation types by three times; however, these differences were not significant ($x^2 = 4.6$, $P = 0.20$, df = 3; see Fig. 3). In 2016, we did not detect significant differences in Southern Plains woodrat activity between vegetation types ($x^2 = 1.4$, $P = 0.71$, df = 3). We also did not detect significant differences between northern grasshopper mouse (*Onychomys leucogaster*) activity across vegetation types in either 2015 ($x^2 = 2.8$, $P = 0.43$, df = 3) or 2016 ($x^2 = 2.1$, $P = 0.56$, df = 3), but activity was consistently higher in woodlands (2015: x̄ = 6.01, SE = 1.53; 2016: x̄ = 3.84, SE = 1.10; see Fig. 3) and decreased as vegetation type changed from shrub dominated to grass dominated. We did not detect significant differences in activity between vegetation types for hispid cotton rats (*Sigmodon hispidus*) and Mexican ground squirrels (*Ictidomys mexicanus*) in 2015 and 2016 at α = 0.05. We did observe activity that was consistently higher in shrubland (2015: x̄ = 0.02, SE = 0.02; 2016: x̄ = 5.15, SE = 2.61) and woodland (2015: x̄ = 0.03, SE = 0.02; 2016: x̄ = 3.58, SE = 1.98) vegetation types than grassland (2015: x̄ = 0.00, SE = 0.00; 2016: x̄ = 0.00, SE = 0.00) and early seral (2015: x̄ = 0.00, SE = 0.00; 2016: x̄ = 0.00, SE = 0.00) for hispid cotton rats in both years (see Fig. 3). We also observed greater activity in woodlands than other vegetation types for Mexican ground squirrels.

Table 4
Model selection results from regression analysis of predation probability and vegetation variables for snakes monitored with nest cameras in four vegetation types on San Antonio Viejo Ranch, Texas, 2015–2016.

Predator type[1]	Model[2]	K[3]	LL[4]	AIC_c[5]	ΔAIC_c[6]	w_i[7]
Snake						
	Shrub	2	−32.01	70.02	0.00	0.52
	Null	1	−34.87	72.31	2.29	0.17
	Julian	2	−33.32	72.64	2.63	0.14
	Concealment	2	−34.02	74.04	4.03	0.07
	Edge	2	−34.26	74.53	4.51	0.05
	Yr	2	−34.62	75.24	5.23	0.04
	Shrub ● concealment	4	−31.07	80.14	10.12	0.00
	Shrub ● edge	4	−31.60	81.19	11.18	0.00
	Global	6	−29.31	112.63	42.61	0.00

[1] Predator type as determined by taxonomic class.
[2] Explanatory variable abbreviations: Null, null model; Shrub, percent shrub cover at nest site; Concealment, percent of nest obscured by vegetation; Edge, distance to closest edge in meters; Yr, year sampled; Julian, Julian date; Global, all variables included.
[3] Total parameters in model.
[4] Log likelihood.
[5] Akaike's information criteria corrected for small sample sizes.
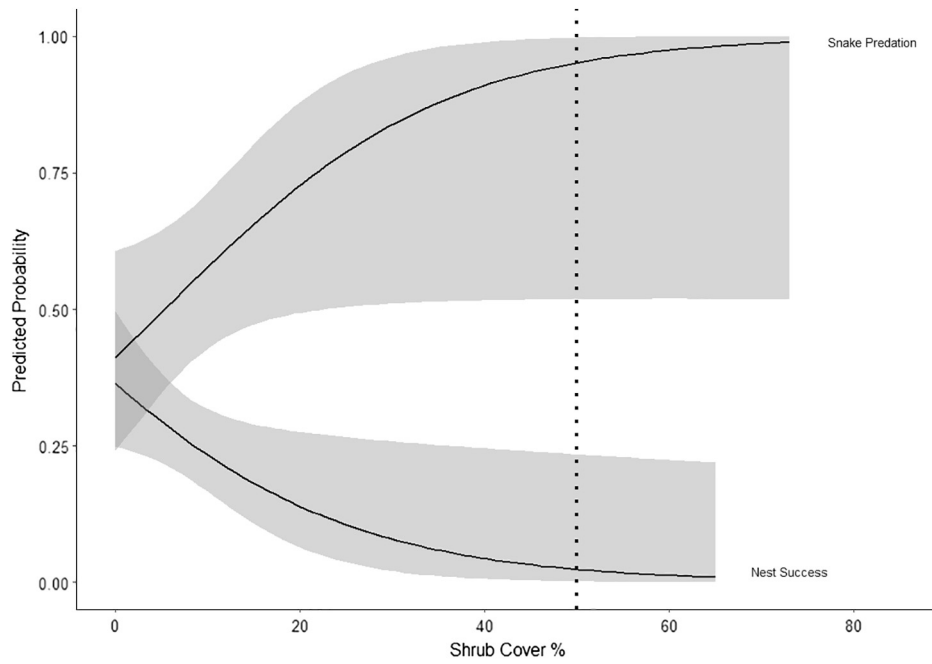[6] AICc relative to the best-fit model.
[7] Model weight.

Figure 2. Relationship between predicted probability of snake predation by Great Plains rat snake *(Pantherophis emoryi)* and coachwhip *(Masticophis flagellum)* at camera-monitored nests, predicted nest success of all monitored medium-sized, cup-shaped nests and percentage of shrub cover at the nest site with 95% confidence intervals and threshold line for nests monitored on San Antonio Viejo Ranch, Texas, 2015–2016.
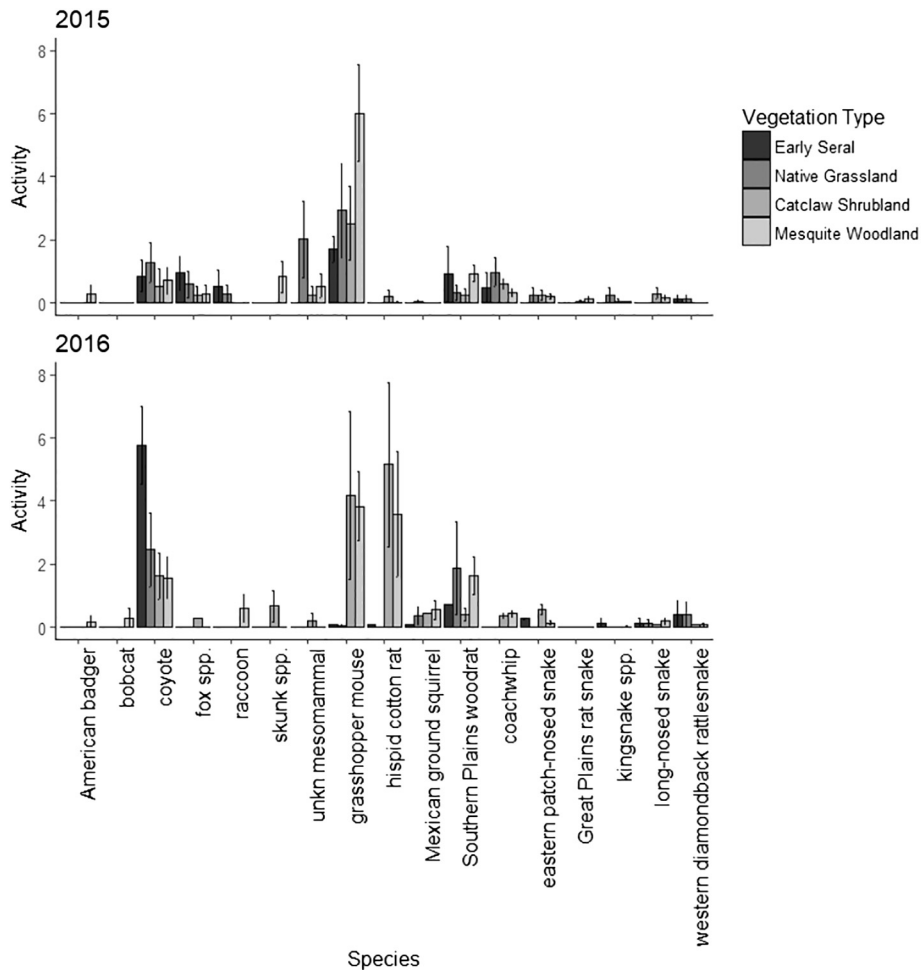

Figure 3. Mean activity (detections per 100 trap nights) and standard error bars for potential nest predator species in early seral, native grassland, catclaw shrubland, and mesquite woodland vegetation types on San Antonio Viejo Ranch, Texas, 2015 and 2016.

We sampled snakes for a total of 5 811 d in 2015 and 6 292 d in 2016. Because we did not detect significant differences in activity between years for any snake species, we pooled snakes across year when statistically evaluating differences in activity between vegetation types. Snake activity we observed was highest in shrubland vegetation types for eastern patch-nosed snakes (*Salvadora grahamiae*; x̄ = 0.05, SE = 0.02), long-nosed snakes (*Rhinocheilus lecontei*; x̄ = 0.03, SE = 0.01), Great Plains rat snakes (x̄ = 0.03, SE = 0.03), and coachwhips (x̄ = 0.50, SE = 0.11), which was consistent with snake nest predators we detected on camera (see Fig. 3). In addition, we observed greater western diamondback rattlesnake (*Crotalus atrox*; x̄ = 0.03, SE = 0.03) and kingsnake (*Lampropeltis spp.*; x̄ = 0.03, SE = 0.03) activity in vegetation types dominated by grasses. However, we did not detect significant differences in activity for these species between vegetation types at α = 0.05.

Discussion

Small increases in percent shrub cover had a negative effect on the success of medium-cup nests. As such, shrub encroachment could have substantial negative effects on birds in the region that have this nest type (e.g., pyrrhuloxia [*Cardinalis sinuatus*]). Great Plains rat snakes were the predominant predator of medium-cup nests in our study, and these snakes have been shown to aggregate in areas of woody cover (Klug et al., 2010). Furthermore, predicted snake predation probability and predicted nest success of medium-cup nests in our study responded in similar magnitudes (albeit inversely) to increases in shrub cover. These models also indicate a critical threshold of shrub cover ($\approx 50\%$), which could be used as a valuable tool when developing land management strategies for breeding birds in this region.

Our hypotheses examining the effects of nest-site vegetation characteristics on nest success (Objective 1) were not supported because concealment and distance to edge were not predictors of nest success during our study. Julian date did have a significant influence on nest success of our medium-cup nest type, and we suspect this may be due to vegetation growth throughout the season increasing visual obstruction of nests (Stauffer et al., 2011). Therefore, using additional methods to quantify concealment (e.g., climate data) may help elucidate these relationships. In addition, avian predation accounted for 50% of events at small-cup nests; therefore, other metrics such as nest height or nest stage may play an important role in driving nest success of this nest type (e.g., Conkling et al., 2012). For our exposed nest type, we found significant differences in success between years, indicating that the exposed nature of these nests could make them more susceptible to abiotic variables such as rain and temperature, which vary from year to year (Skagen and Adams, 2012). Although not recorded on camera, we did observe several exposed nests abandoned after heavy rain, so these nests may be more susceptible to weather events. Mean rainfall during our study period did not differ between years; however, peak rainfall occurred later in 2016 when compared with 2015 (May as opposed to March; PRISM Climate Group, 2017); thus, reduced nest success in 2016 may be due to timing of precipitation.

Predator detections at camera-monitored nests (Objectives 2 and 3) were variable across vegetation types. Coyotes, our predominant mesomammalian and large mammalian nest predator, generally depredated nests with low shrub cover at the nest site and vegetation type scale, as hypothesized. Coyotes also depredated nests with the shortest distance to edge relative to other predators, further supporting our hypotheses. Woody vegetation could increase visual obstruction of nests, thus decreasing predation by these predators. In addition, coyotes use roads and forest edges as travel routes and for foraging (Heske, 1995; Kuehl and Clark, 2002), thus mesomammalian and large mammalian predators such as coyotes are likely to depredate nests closer to edges. We also observed half of coyote predation events at roadrunner nests, likely due to size and placement of nests.

Our avian predator type had the highest species richness of any other group; therefore, relationships between predation and vegetative characteristics may not be apparent. Even so, we observed that avian predation events were not influenced by woody cover at the vegetation type scale; however, predation events did increase with woody vegetation cover at the nest-site scale. We suspect avian predators likely use woody vegetation for perching locations (Bergin et al., 1997), which may explain these observations. Concealment of nests depredated by avian predators did not differ from other predators, yet avian predators generally depredated nests closer to an edge. As we hypothesized, avian predators may use edges for movement and perching locations to view prey.

Snake predation at the vegetation type scale was highly variable and species specific; however, we did observe increased Great Plains rat snake and coachwhip predation with increases in shrub cover at both vegetation and nest-site scales, supporting our hypotheses. This likely explains the decreases in nest success with increased shrub cover in the medium-cup nest type as previously discussed. We did not, however, expect for mean shrub cover to be as low as 15% for nests depredated by snakes, although this observation is consistent with other studies examining similar snake species in Kansas tallgrass prairies (Klug et al., 2010). In addition, we did not observe any effect of edge on snake predation even though it is an important component of snake habitat (Sperry et al., 2008; Weatherhead et al., 2010). A potential explanation for this is that the extreme heat in south Texas may drive both Great Plains rat snakes and coachwhips away from edges and into more densely wooded areas for thermoregulation, even at night. We suspect rat snakes depredated nests predominantly at night due to hot temperatures and even though coachwhip predation events occurred exclusively during the day, they likely hunted in woody areas away from exposed edges for thermoregulation purposes (Halstead et al., 2009).

We observed only two ant predation events on camera, which was surprisingly low due to the prevalence of invasive fire ants in south Texas. We did not sample for fire ant activity in our study; however, we would regularly encounter ant hills when searching for and checking nests. Previous research has indicated that despite their abundance and prevalence in Texas, ant impacts vary regionally (Champomizzi et al., 2009; Conkling et al., 2012).

Predator activity was variable across vegetation types (Objective 4) and was not a reliable predictor of nest success or predation risk. Mesomammal and large mammal activity was generally higher in vegetation types dominated by grasses than woody plants; however, these differences were not statistically significant for coyotes. Coyote activity did not reflect coyote frequency at camera-monitored nests. In our study, the role of other mesomammal and large mammal predators in nest success of birds in this region was negligible.

Small mammal activity was generally higher in vegetation types dominated by woody cover, thus supporting our hypothesis. This relationship, however, was not observed at camera-monitored nests. Research indicates small mammal activity is driven by smaller-scale vegetative features (Thompson and Gese, 2013) and food availability, which may be an explanation for our results (Reed et al., 2005; Schorr et al., 2007). Despite the high levels of small mammal activity we documented in both 2015 and 2016, we only observed one small mammal predation event at a camera-monitored nest. A possible explanation for this was abundant alternative food resources being available during the bird nesting period. Both grasshopper mice and Mexican ground squirrels are known to forage primarily on insects (Edwards, 1946; Horner et al., 1964). Ample insects and forbs for small mammals to forage on could be a potential explanation for why small mammal activity did not reflect nest predation in our study. In addition, we likely underestimated Mexican ground squirrel activity because we sampled predominately at night and ground squirrels are known to forage during the day (Schmidley, 1994).

Lastly, snake activity was variable, depending on the species of snake. Snakes were more active in vegetation types dominated by woody cover, supporting our hypothesis, and remaining consistent

with snake predation events recorded on camera-monitored nests. Activity for Great Plains rat snakes at sampling locations was low, given that these snakes depredated 33% of all camera nests. Because rat snakes have the potential to be large bodied, the sampling method we used may not adequately sample for this species (i.e., larger-bodied snakes may not fit in funnel traps or easily escape from pitfall traps). Coachwhip activity was highly variable; however, we did have greater success trapping these species, likely because their bodies were slender enough to fit into our traps. Even so, snake activity was not a valuable indicator of predation risk in our study.

Implications

Our results suggest that woody encroachment in south Texas rangelands likely produces negative effects on nesting birds. Even slight increases ($\approx$10%) in shrub cover resulted in significant increases in nest failure, most likely caused by snake predation. However, woody vegetation clumps (mottes) do offer important locations for breeding, refuge, and foraging for birds and other native wildlife species. Thus, land managers in this region should maintain savanna ecosystems with open grasslands and sparse mesquite mottes. In addition, these mottes should ideally have approximately 10% shrub cover per 100 m^2 and not exceed 60% per 100 m^2 to discourage snake predation. Because the majority of predators were rat snakes, preventing savannas (e.g., controlled grazing, prescribed fire, brush control) from maturing and transitioning to woodlands should reduce snake nest predation and increase nest success.

Finally, our study indicates the importance of local-scale research for aiding land owners in managing wildlife populations. Several hypotheses based on our review of similar studies conducted in other areas of the United States were not supported by our data. Thus, there likely is not a formula for predicting predation at levels greater than the ecoregion scale. Wildlife biologists should work closely with land owners to help predict the effects of land management on wildlife species. Understanding how vegetation management drives predator assemblage and nesting success at the local scale is paramount to conserving these species.

Acknowledgments

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