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Source: Journal of Wildlife Management, 70(2):564-571. 2006.

Published By: The Wildlife Society-2

DOI:

URL: <http://www.bioone.org/doi/full/10.2193/0022-541X%282006%2970%5B564%3AFINBNS%5D2.0.CO%3B2>

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Factors Influencing Northern Bobwhite Nest-Site Selection and Fate

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Abstract

Understanding factors underlying nest-site selection is important for effective conservation and management of a declining and economically important species. We measured vegetation characteristics at nest sites of northern bobwhites (*Colinus virginianus*; hereafter, bobwhites) and at random points in the Texas Panhandle. We used these data to develop a neural network classification model for predicting nest-site suitability. We also compared the characteristics of successful nests with those of failed nests using the bootstrapping method. We monitored a subset of nests using video cameras during incubation and for 3 days postcompletion (succeeded or failed) to determine nest fate, cause of fate, and nest activity after completion. Nest-canopy height, percent shrub cover, and bare-ground exposure were important vegetation characteristics influencing nest-site selection. Sites became more suitable as canopy height exceeded 40 cm, shrub cover exceeded 25%, and as bare-ground exposure fell below 30%. Successful nests had higher canopies and more shrub cover than failed nests, but successful nests had more bare ground than failed nests. Nest visits were common at monitored nests after nest completion (failed, successful). Most visitors were adult bobwhites, but other species also visited nests. Such visits might bias the determination of nest fate if the determination is based on nest remains, especially if nests are not monitored daily. Bobwhites might select nest sites to maximize nest concealment compared with random locations. (THE JOURNAL OF WILDLIFE MANAGEMENT 70(2):564–571; 2006)

Key words

Colinus virginianus, nest fate, nest-site selection, neural network modeling, northern bobwhite.

The outcome of a nesting attempt often depends in part on the placement of the nest in the environment. Nest placement influences the risk of nest predation (Ricklefs 1969, Martin 1993a) and the microclimate experienced by the developing embryo and chick (With and Webb 1993, Gloutney and Clark 1997, Nelson and Martin 1999). Because parental fitness is a direct function of breeding success, natural selection should favor nest-placement strategies that maximize the chances of successfully fledging offspring, especially for ground-nesting species in grasslands, which experience high levels of predation (Martin 1993b). A characterization of the habitat features used by adults in selecting nest sites allows an understanding of the factors influencing fitness. In practical terms, such knowledge allows for more effective conservation and management by allowing habitat manipulations to be tailored to the specific nesting needs of a particular species.

Although the expectation is that nesting adults will select nest sites that maximize their fitness, this is not always the case in human-altered environments. For example, Misenhelter and Rotenberry (2000) reported that the fitness of sage sparrows (*Amphispiza belli*) was lower in preferred habitats than in nonpreferred habitats. Blackcaps (*Sylvia atricapilla*) in the Czech Republic also preferentially selected nesting habitat in which their nesting success was lower than in nonpreferred, natural habitats (Remeš 2003). Those authors hypothesize that human-induced

changes to habitats have decoupled habitat selection from suitability. In the case of the sage sparrow, the decoupling occurred through concurrent changes in the nest-predator community leading to higher nest predation in preferred habitats. For blackcaps, the decoupling occurred because of differences in the phenology of native, floodplain forests and exotic, black locust (*Robinia pseudoacacia*) plantations causing adults to select inferior exotic habitats that leaf-out earlier than native forests. Therefore, an analysis of the characteristics of successful and failed nests is an important component of our understanding of nest-site selection. Knowledge of the factors influencing nest success allows conservation actions that do not exacerbate declines of certain species by manipulating habitat that is preferred, but which reduces production. That is, such knowledge will help conservation managers avoid creating sink habitats.

Although a large body of descriptive studies exists on the nesting habitat of bobwhites (e.g., Klimstra and Roseberry 1975, Roseberry and Klimstra 1984), only Townsend et al. (2001) have compared habitat characteristics between nests and random points. Our study contributes to a broader understanding of nest-site selection by showing how bobwhites choose nest locations in heterogeneous landscapes, something that cannot be accomplished with simple descriptive studies. Our study also compliments that of Townsend et al. (2001) by showing that similar patterns are apparent at disparate locations within the geographic range of the bobwhite, which increases the level of confidence in the results (Johnson 2002). Townsend et al. (2001) reported that nest sites were located at points with greater structural complexity than random points. Further, successful nests were more concealed than failed nests. Hernández et al. (2003) reported partial support for the hypothesis that bobwhites

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selected nests sites that provided structural protection against depredation. However, Bowman and Harris (1980) reported experimental results indicating that spatial heterogeneity rather than concealment was the important factor in reducing nest predation.

As noted above, few studies have compared bobwhite nest sites to randomly available points. Our objective, therefore, was to develop a neural-network model of bobwhite nest-site selection for discriminating nest sites from random points and for increasing our understanding of the factors influencing site selection in heterogeneous landscapes. We also compare the characteristics of successful nests (those fledging ≥ 1 chick) with characteristics of failed nests using bootstrapping. We end by discussing differences in nest characteristics among those lost to different nest predators as determined from video-monitored nests.

Study Area

We obtained data as part of a 2-year study of bobwhite ecology on the Mesa Vista Ranch in Roberts County, Texas, USA. This 11,330-ha ranch, managed for bobwhite production, is located along the breaks of the Canadian River in the Great Plains physiographic region (Jordan et al. 1984). This area has a steppe-type climate with a 220-day growing season (Jordan et al. 1984, Odintz 1996). A 796-ha subsection of the ranch was used for data collection and was selected based on the diversity of habitat types present. Native grasses included western wheatgrass (*Agropyron smithii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and big bluestem (*Andropogon gerardii*). Woody species included sand sagebrush (*Artemisia filifolia*), hackberry (*Celtis* spp.), sand plum (*Prunus augustifolia*), and lemon sumac (*Rhus trilobata*).

Methods

Field Methods

We captured bobwhites using night lighting (Huempfer et al. 1975) year round and using walk-in funnel traps (Stoddard 1931) during the autumn and winter. Traps were placed near access roads in areas frequented by bobwhites. We checked traps twice daily to minimize the time each bird spent in a trap. We followed protocols approved by the Institutional Animal Care and Use Committee at Oklahoma State University.

All captured bobwhites weighing ≥ 110 g were fitted with aluminum leg bands bearing a unique identification number. Bobwhites weighing ≥ 150 g were also fitted with 6-g necklace-style radiotransmitters (American Wildlife Enterprises, Monticello, Florida) equipped with either a mortality- or temperature-sensing transmitter. Both types of collars had mean life-expectancies of 6 months. We recorded the sex, age, mass, and condition of each bobwhite at time of capture. Sex and age were determined from standard references (Stoddard 1931, Stokes and Stokes 1996, Dimmick and Pelton 1994), and mass was measured using a spring scale (Pesola AG, Baar, Switzerland).

We located radiomarked bobwhites by triangulation (White and Garrott 1990) 2–7 times per week to maximize the chances of finding nest locations. If a bobwhite was located in the same area for 2 consecutive days, the area was thoroughly searched for possible nests. After locating the nest, the nesting adult was

identified. We recorded a general description of the nesting habitat and obtained the UTM coordinates of the nest from a hand-held GPS unit (Trimble Navigation, Sunnyvale, California). We recorded the number of eggs only if the attending adult was not present at the nest to minimize disruption.

We had 5 video camera units. Therefore, of located nests, 5 were chosen randomly for video monitoring. The video units consisted of a waterproof, black-and-white infrared camera, time-lapse video cassette recorder housed in a waterproof case, a marine battery, and solar panel. The time lapse used 3-second intervals so that 24 hrs of nest time could be recorded on a standard 8-hr videocassette. We placed cameras 0.5 m from nests when the attending adult was off the nest (Pietz and Granfors 2000). Video units were checked daily throughout the nesting period and for 3 days past nest completion, regardless of nest fate. We then assigned video units to new nests, and the process was repeated until the end of the nesting season. We used a sweep-sampling method with a 10-min sampling interval to analyze videos (Martin and Bateson 1986). If nests failed, tapes were scan-sampled to observe the cause of failure (e.g., predator). When a nest without a video unit failed, we listed the cause of failure as unknown because of the difficulty in assigning failure to particular agents (Larivière 1999).

Following nest completion (success, fail), we measured the vegetation characteristics of the nest area. An equal number of randomly chosen, non-nest sites were also sampled. Because bobwhites are not territorial during the nesting season and only defend the immediate nest area, we selected random sites by randomly rotating a compass to obtain an arbitrary bearing and following that bearing for 60 m away from the nest site. Twelve vegetation measurements were recorded for each nest and random site (Table 1). Cover variables were estimated using 1-m² quadrats centered over nests or random points. Screening cover was assessed using a profile board (Nudds 1977) viewed at 7 m from the sample point in each of the cardinal directions and by averaging the 4 measurements. The angle of obstruction was measured along 8 compass radii centered on the sample point and

Table 1. List of vegetation variables and their definitions used to predict nest-site selection by bobwhites on the Mesa Vista Ranch, Roberts County, Tex., USA, 2001–2002. Asterisks after variable names indicates variables retained in the model after initial screening. Variables not retained had relevance scores below 5% on initial training attempts.

Variable	Definition
Canopy height*	Height of vegetation above nest or random point (cm)
Tallgrass*	Percent cover by the dominant tallgrass
Midgrass	Percent cover by the dominant midgrass
Shortgrass	Percent cover by the dominant shortgrass
Forbs	Percent cover by the dominant forb
Shrubs*	Percent cover by the dominant shrub
Bare-ground exposure*	Percent of ground unobstructed by vegetation or litter
Angle of obstruction	Mean angle measured along 8 radii from nest or random point and surrounding vegetation
Screening cover 10	Percent visual obstruction of a profile board 0–10 cm
Screening cover 20	Percent visual obstruction of a profile board 11–20 cm
Screening cover 30	Percent visual obstruction of a profile board 21–30 cm
Mean screening cover*	Arithmetic mean of the three screening-cover classes at each point

was then averaged. The angle of obstruction is the angle between the sample point and the top of the surrounding vegetation (Kopp et al. 1998).

Data Analysis

We used a neural network modeling approach for the analysis of nest-site selection. Neural network models are a type of machine-learning algorithm (Smith 1996, Fielding 1999a) that has been shown to be more powerful than traditional statistical methods for both classification and predictive problems (Paruelo and Tomasel 1997, Olson and Cochran 1998, Manel et al. 1999). Ecological applications of this technique include models of algal blooms (Recknagel et al. 1997, Maier et al. 1998), of bird-species distribution (Manel et al. 1999), and of the abundance of northern bobwhites (Lusk et al. 2001). A neural network model is nonparametric and is not affected by multicollinearity. Furthermore, a neural network model can be applied to linear and nonlinear relationships without a priori specification of the functional form of the relationship. However, the inherent complexity of the neural network model makes interpretation of the model output difficult and requires the use of simulations to render the output biologically interpretable.

A backpropagation neural network model (Smith 1996) was developed using QNet 2000 (Vesta Services, Winnetka, Illinois). This type of neural network model is described in detail elsewhere (Smith 1996). The dataset consisted of bobwhite nests and paired random locations ($n = 110$, 55 nests and 55 random locations). We divided the data into training ($n = 88$) and testing ($n = 22$) data sets before analysis by selecting 11 cases each from nest and random points. This selection method ensured that the 2 data sets would be balanced with respect to nest and random locations (Fielding 1999b). Training data were used to develop the neural network models. Testing data were used to assess the accuracy of the model predictions during the training process but had no influence over weight adjustment and, therefore, assessed the accuracy of the model when presented with novel data.

We trained a series of models identical except in the number of neurons. This procedure identified the optimum number of neurons for the classification problem. The model with the fewest processing elements and the highest correlation between observed and predicted classifications was selected. All models were run for 500 iterations. During these initial trials, several variables were consistently small contributors to model predictions (relevance $< 5\%$, see below). Therefore, the uninformative variables were removed from the model to increase parsimony. Canopy height, percent cover of tallgrasses, percent shrub cover, bare-ground exposure, and mean percent screening cover were retained as variables in the model (Table 1). The optimization procedure was repeated with the reduced variable list.

We quantified the accuracy of the selected neural network model using a receiver operating characteristic plot (ROC; Fielding and Bell 1997, Fielding 1999b). The area under the curve of the ROC plot is a threshold-independent measure of the accuracy of the model and, therefore, is preferred to traditional accuracy measures such as percentage correctly classified. That is, the area under the curve is not dependent on an arbitrary cutoff point for determining class membership (e.g., 0.5) but is based on the relative difference between classification scores between groups.

The area under the curve can be interpreted as the proportion of times a randomly selected nest point (coded as 1.0) would receive a higher classification score than a randomly selected random point (coded as 0.0). This analysis was performed for both training and testing output using SYSTAT v10.2 (SYSTAT Software, Chicago, Illinois).

To determine the relative importance of the remaining variables in the model and investigate the influence of these variables on nest-site selection, we calculated a relevance score and used simulations for each variable. The relevance of a variable is its percent contribution to model predictions and is calculated as the sum of squared connection weights for the variable of interest divided by the sum of squared connection weights of all variables (Özesmi and Özesmi 1999, Gevrey et al. 2003). Simulations investigated the change in the neural network classification scores across the observed range of the variable of interest. To accomplish this, a series of datasets was created in which the variable of interest (e.g., canopy height) varied incrementally between the maximum and minimum observed values while all other variables were held constant at their mean. The neural network model was then used to generate predicted classification scores that were plotted against the variable of interest. For simulations, an arbitrary dichotomy of 0.5 was selected as a convenient reference for interpreting the model output because prediction accuracy was not relevant for the simulations (Fielding and Bell 1997, Guthery et al. 2001).

Because there were unequal numbers of successful and failed nests, we used bootstrapping to investigate differences between the nest-site characteristics of both types of nests. A distribution of means was obtained by generating 1,000 bootstrapped means for each variable of interest (Mooney and Duval 1993). Bootstrap means were calculated using the same number of cases as the original data (successful nest, $n = 15$; failed nests, $n = 39$). We report results as means \pm SE, unless otherwise noted. The 95% confidence intervals were used to test for differences between successful and failed nests (Mooney and Duval 1993).

Results

During the breeding seasons of 2001 and 2002, 26 and 33 nests were monitored, respectively. Of the monitored nests, $26.9 \pm 8.9\%$ were successful (apparent success) in 2001, and $39.4 \pm 8.6\%$ were successful in 2002. Hens averaged 1.7 ± 0.3 nesting attempts in 2001 and 1.4 ± 0.2 nesting attempts in 2002. Predators, including mammalian carnivores (raccoon [*Procyon lotor*], striped skunk [*Mephitis mephitis*], coyote [*Canis latrans*], and badger [*Taxidea taxus*]) and unidentified snakes, accounted for $64.4 \pm 11.0\%$ of nest losses in 2001 and $45.0 \pm 11.4\%$ in 2002 based on video evidence (Table 2). No avian predators were recorded depredating monitored nests. The overall abandonment rate for the 2 years was $11.9 \pm 4.3\%$, of which only 1 case of abandonment occurred before camera set-up.

Observations made during the 3 days after nest completion, either as successful or failed, showed that 101 visits to nests were made. Adult bobwhites, alone or accompanied by another adult, were the most frequent visitors after the cessation of nesting activity (Table 3). Visits by species other than adult bobwhites averaged 2.1/nest in both years. Most of these visits (1.1 visits/

Table 2. Nest fates as percentage of losses to a particular agent for bobwhites on the Mesa Vista Ranch, Roberts County, Tex., USA, 2001 ($n = 26$) and 2002 ($n = 33$).

Fate	2001	2002	Years pooled
Successful	26.9	39.4	33.8
Raccoon	11.5	3.0	6.8
Striped skunk	11.5	9.1	10.2
Coyote	11.5	3.0	6.8
Badger	3.8	3.0	3.3
Snakes	11.5	9.1	10.6
Abandonment	7.7	15.2	11.9
Unknown	11.5	18.2	15.3

nest) were made by rodents. For example, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) made 21 postnest-fate visits (Table 3), during which eggs were removed 17 times. It was usual for nest visitors to remove only a portion of the contents rather than the entire contents; in only 1 case did a ground squirrel remove all eggs left in a nest.

A neural network model consisting of 2 neurons was found to be optimal for our application. This model accounted for 40.1% of the variation in the training data and 43.6% of the variance in the testing data. The area under the curve of the ROC plot was 0.842 for the training data and 0.768 for the testing data. Therefore, a randomly chosen nest from the training dataset would receive a higher neural network classification score than a randomly chosen random point 84.2% of the time. Likewise, a randomly chosen nest from the testing data would receive a higher neural network classification score than a randomly selected random point 76.8% of the time. Stated differently, there was an 84.2% probability of correctly classifying each of a pair of points as random or nest using the neural network model based solely on the relative difference in their classification scores.

Canopy height was the most important variable for distinguishing between nest and random points, followed by shrub cover and bare-ground exposure (Table 4). Those variables had a combined relevance score of 91%. Tall-grass cover and mean screening-cover contributed <10% to the model predictions. Simulations were conducted on the 3 most important variables in the model. Classification scores increased with canopy height and shrub

Table 3. Frequencies of postcompletion (3 days) nest visits by species for failed ($n = 19$) and successful ($n = 10$) nests of bobwhites on the Mesa Vista Ranch, Roberts County, Tex., USA, 2001–2002.

Species	Failed	Successful
Incubating bobwhite	36	2
Other bobwhite ^a	2	1
Thirteen-lined ground squirrel	16	5
Unknown rodent	4	6
Unknown snake	3	5
Raccoon	4	1
Snake	13	8
Striped skunk	2	0
Badger	1	0
Coyote	1	0
White-tailed deer (<i>Odocoileus virginianus</i>)	1	0

^a Any adult bobwhite other than the incubating adult, unless accompanied by the incubating adult. Four nests received visits from the incubating adult with another adult bobwhite.

Table 4. Relevance scores (percent contribution) and mean values at nest sites for variables used to train the neural network model to discriminate between nest and random locations at the Mesa Vista Ranch, Roberts County, Tex., USA, 2001–2002.

Variable	Relevance (%)
Canopy height (cm)	32.9
Shrub cover (%)	31.2
Bare-ground exposure (%)	26.9
Mean screening cover (%)	4.6
Tall-grass cover (%)	4.5

cover; therefore, nest sites had greater canopy heights and more shrub cover than random points. Using a 0.5 cutoff threshold, points with canopies shorter than approximately 40 cm were unsuitable for nests, as were those with shrub cover below approximately 25% (Fig. 1). Classification scores decreased with increasing bare-ground exposure (Fig. 1). A point became unsuitable for a nest site as bare-ground exposure exceeded approximately 30% (Fig. 1). We regressed date of initiation against bare-ground exposure to determine whether any temporal trends in patterns of bare-ground exposure might have confounded our results. We found no relationship between the amount of bare ground and the timing of nest initiation ($P = 0.3712$).

The 95% confidence limits on the bootstrapped means for canopy height, shrub cover, and bare-ground exposure at

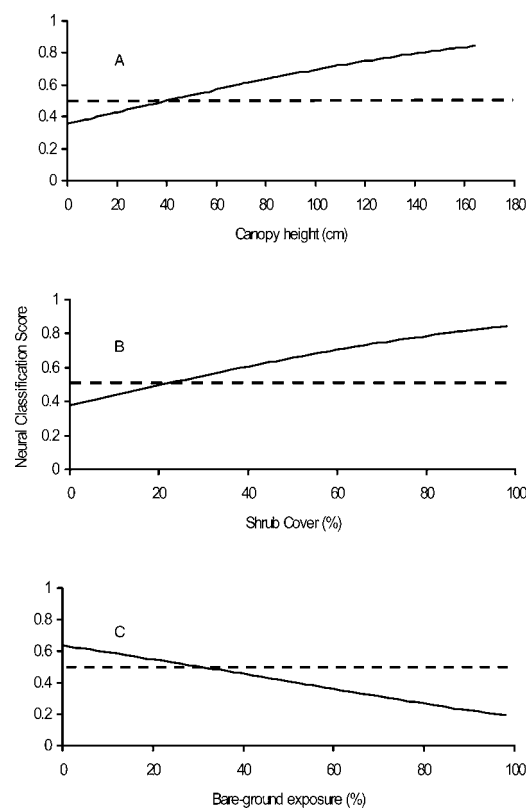


Figure 1. Simulation results from the trained neural-network model for differentiating random and nest locations based on vegetation characteristics. Results are presented only for variables with >10% contribution to model output: (A) canopy height (cm), (B) percent shrub cover, and (C) bare-ground exposure (%). Dashed horizontal lines represent an arbitrary 0.5 cutoff threshold between suitable and unsuitable.

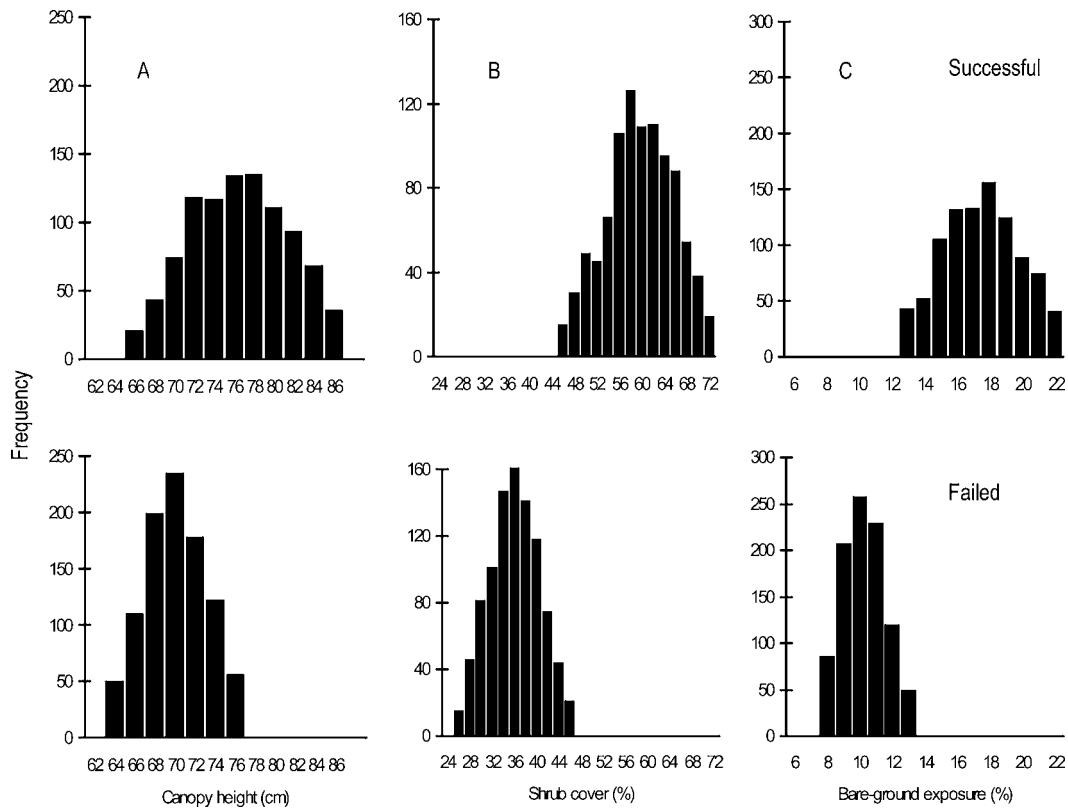


Figure 2. Frequency histograms showing the results of the bootstrap analyses comparing successful (top row) and failed (bottom row) nests. Each histogram represents the distribution of bootstrapped means. Results are presented only for variables with >10% contribution to model output: (A) canopy height, (B) percent shrub cover, and (C) bare-ground exposure (%).

successful and failed nests overlapped, indicating that the differences were not significant (Fig. 2). Although not statistically significant, we believe that the differences were biologically significant. Failed nests tended to have shorter canopy heights than successful nests. There was less overlap between successful and failed nests with regards to shrub cover and bare-ground exposure than for canopy height. Successful nests tended to have more shrub cover and more bare-ground exposure than failed nests (Fig. 2).

The suite of observed nest predators consisted mostly of mammals but included snakes (Table 2). Characteristics of nests depredated were similar among predator classes (Table 5). However, small samples within each predator category prevented a statistical comparison of vegetation characteristics among predators. Nest canopy height was shortest on nests depredated by badgers (45.5 ± 4.5 cm, $n = 2$) and tallest on those depredated by raccoons (85.4 ± 12.0 cm, $n = 5$). Percent cover by shrubs was lowest for nests depredated by snakes (25.2 ± 8.0 %, $n = 6$) and

greatest for nests depredated by raccoons (64.0 ± 16.6 %, $n = 5$). Finally, bare-ground exposure was lowest at nests depredated by raccoons (2.3 ± 0.6 %, $n = 5$) and greatest at nests depredated by badgers (26.8 ± 10.8 %, $n = 2$). Grouping predators into predator guilds based on taxonomic class (mammal, reptile) revealed no significant patterns; we again compare the vegetation characteristics between the 2 groups. Nest-canopy height (74.6 ± 6.0 cm, $n = 16$), percent shrub cover (49.8 ± 8.5 %), and bare-ground exposure (11.1 ± 2.5 %) were greater at mammal-depredated nests than at snake-depredated nests (56.0 ± 6.0 cm, 25.2 ± 8.0 %, and 6.1 ± 3.0 %, respectively; $n = 6$).

Discussion

Our results showed that nest-canopy height, percent shrub cover, and bare-ground exposure were the most important vegetation characteristics of those measured for determining the suitability of a particular location for nesting. These variables could reflect aspects of nest concealment, which can afford nests protection

Table 5. Mean values (\pm SE) of vegetation variables at failed nests averaged for each mortality source, Mesa Vista Ranch, Roberts County, Tex., USA, 2001–2002.

Predator/variable	Canopy height (cm)	Tallgrass cover (%)	Shrub cover (%)	Bare ground (%)	Mean screening cover (%)
Raccoon	85.4 (12.0)	0.0 (0.0)	64.0 (16.6)	2.3 (0.6)	96.3 (2.9)
Badger	66.0 (9.7)	0.0 (0.0)	50.3 (12.8)	26.8 (10.8)	96.3 (3.8)
Coyote	73.3 (15.1)	9.5 (9.5)	53.0 (18.5)	12.0 (4.0)	89.6 (5.0)
Skunk	76.6 (5.2)	22.5 (9.2)	32.8 (15.6)	12.8 (2.5)	96.9 (1.0)
Mammals (pooled)	74.6 (6.0)	9.4 (4.2)	49.8 (8.5)	11.1 (2.5)	94.8 (1.7)
Snakes	56.0 (6.0)	25.5 (10.1)	25.2 (8.0)	6.1 (3.0)	90.7 (1.9)

from predators and possibly thermal stress. Therefore, nest concealment could be a factor determining the suitability of a point as a nest site: the neural network classification scores increased with increases in nest-canopy height and percent shrub cover but declined with increases in bare-ground exposure. These results are similar to descriptive findings reported in the literature. Errington (1933:123) recognized the importance of vegetation structure in nest concealment for nesting bobwhites, commenting that "... almost any herbaceous vegetation, open yet affording concealment, may be utilized." He reported that 80% of nests ($n = 65$) were found in vegetation sufficiently thick as to provide a closed roof over the nest cup (Errington 1933). Similarly, Klimstra and Roseberry (1975) found that 85% of nests contained a full, closed canopy over the nest. The mean height of nest vegetation was 49.5 cm (Klimstra and Roseberry 1975; $n = 317$), which is similar to the value of 40 cm obtained from the neural network model marking the threshold between suitable (>40 cm) and unsuitable (≤ 40 cm) locations. However, despite the preponderance of nests enclosed by canopies in their sample, Klimstra and Roseberry (1975:28) reported that the presence or amount of canopy did not appear to affect predation rates.

Townsend et al. (2001) reported greater structural complexity at nest compared to random points. These authors reported that grass (~50%) and woody-plant (20–30%) cover were greater at nest than at random points (~30% and 10–15%, respectively), and the amount of bare ground was lower ($<25\%$ vs. $>28\%$, respectively). Again, these results agree with those reported here. Although the specific variables in the analyses differed from those in the current study, they all are related to nest concealment, whether positively (canopy height and grass, shrub, and woody cover) or negatively (bare-ground exposure). Multiple configurations of multiple structural components can be of equal suitability to a species because they provide the same services—in this case, nest concealment—to the species (Guthery 1999).

Hernández et al. (2003) tested the predictions resulting from 2 hypotheses to explain the use of prickly pear (*Opuntia* spp.) as nesting cover by bobwhites in the Rolling Plains region of Texas. In contrast to the Mesa Vista ranch, which was managed for bobwhites with stocker cattle, the study site in Hernández et al. (2003) was heavily grazed. They found that bobwhites selected prickly pear, which provided nests with structural cover, for nest sites even when abundant bunchgrass was available, but that nest success was independent of nesting substrate. However, nest success was dependent on the level of concealment and protection provided by the nesting substrate, irrespective of plant species. Again, it is the function that the habitat element provides, rather than the habitat element itself, that seems to be the object of selection. As such, the results reported by Hernández et al. (2003) agree with those reported here: they found that bobwhites selected nest sites that offered concealment and physical protection (i.e., prickly pear thorns) for their nests.

Given the descriptive nature of much of the earlier work on bobwhite nesting ecology, there is little in the literature with which to compare the results of our analysis of nest success. Townsend et al. (2001) provided an analysis analogous to that provided herein. They also report a lack of significant differences between vegetation variables at successful and failed nests. However, the extent of

overlap for the variables in the current analysis was small for percent shrub cover and bare-ground exposure (Fig. 2). Percent shrub cover tended to be greater at successful nests than at failed nests (Fig. 2). Likewise, bare-ground exposure was greater at successful nests compared to failed nests (Fig. 2). Successful nests were found under a greater array of canopy heights than failed nests (Fig. 2). That is, the distribution of mean canopy heights was wider for successful than failed nests. One would expect that if nest concealment were the underlying factor guiding nest-site selection for this species, then successful nests would be better concealed than failed nests. Our results seemed to support this expectation, albeit not significantly so: successful nests tended to have more shrub cover and higher canopies than failed nests. However, we expected—given the results of the neural network model—that successful nests would be associated with less bare ground than failed nests. In fact, this is the pattern observed by Townsend et al. (2001). Our results showed the opposite pattern, however: successful nests had higher bare-ground exposure than failed nests. The current result could be due to human alteration of habitat that has dissociated selection criteria (low bare-ground exposure) from expected benefit (nest success). Mesa Vista is managed for bobwhite production and management techniques include grazing, but at such a low intensity as to be inconsequential (Smith 2003). Although grazing reduces litter cover, thereby increasing bare-ground exposure and increasing nest predation by exposing concealed nests (Knopf 1996), grazing is used as a management tool at Mesa Vista and, as such, vegetation removal by cattle might not reach a level at which those detrimental effects manifest. We are, therefore, unable to explain the tendency for successful nests to be located in areas of more bare-ground exposure than failed nests. There might be some factor related to bare-ground exposure that enhances nest success. For example, bare ground might afford some thermal advantage to the nearby nest or might allow adults to spot predators earlier. It seems prudent to investigate this pattern more closely to determine whether it is an artifact of the data and, if not, what are the potential causes of decreased nest success in preferred habitats.

We were unable to conduct a statistical analysis of vegetation characteristics among nests depredated by various predators because of small sample sizes, but noted no overt patterns (i.e., the 95% confidence intervals for means overlapped). This is not surprising because most of the depredation events were due to mammals, which are likely to hunt using similar senses and tactics. When grouped together by taxonomic class, we still found no significant patterns in vegetation characteristics between nests depredated by mammals or by snakes.

The determination of nest predators based on nest remains cannot be accomplished unambiguously (Larivière 1999). We avoided this ambiguity by using cameras at a subset of nests in the sample (Table 2). In many cases, the cause of nest predation determined from sign at the nest was found to be erroneous after determination from videotapes. We also found that various species visit nests after completion. Stake et al. (2004) observed similar post-fate nest visits using video cameras at golden-cheeked warbler (*Dendroica chrysoparia*) nests in Texas. Such visits can disturb nest remains and, thereby, alter the determination of the nest predator and of the fate of the nest, especially when nests are visited only periodically during the study. For example, a

successful nest might be visited by a mammalian predator following departure of the brood, and its activities at the nest might lead a researcher to later classify it as failed and attribute the cause of failure to a mammalian predator.

Management Implications

Our results showed the importance of nest concealment for the selection of nest sites by bobwhites. Although our study was focused on a single site, the similarity of our results with those of Townsend et al. (2001) indicates the generality of the findings. Managers in semiarid rangelands should attempt to create or maintain nesting habitat with a canopy height >40 cm and with shrub cover >25%. Because of the ambiguity with regards to the amount of bare ground, we suggest further research into this matter to determine whether the observed pattern was an eccentricity in our data or whether the pattern is genuine.

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The results reported here also warn against assigning nest predators to apparently failed nests based only on sign left at the nest. Postfate visits by other species could obscure the fate or cause of the loss leading to erroneous conclusions about nest predation. Such conclusions could misdirect management efforts. **We recommend that cameras be used for studies of the causes of nest loss.**

Acknowledgments

Financial support was provided by the Mesa Vista Ranch, Bollenbach Endowment, Grand National Quail Foundation, and Oklahoma Agricultural Experiment Station. B. Pickens, Jr., K. Boone, and the Mesa Vista staff provided support and accommodations during fieldwork. B. Baker, T. Hiller, and T. Puckett provided field assistance. This manuscript was approved for publication by the Oklahoma Agricultural Experiment Station.

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Associate Editor: Brennan.