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LANDSCAPE FEATURES AFFECTING NORTHERN BOBWHITE PREDATOR-SPECIFIC NEST FAILURES IN SOUTHEASTERN USA

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ABSTRACT

Nest predation is a critical component in avian productivity and typically is the leading cause of nest failure for most birds. Several landscape features are thought to drive the behavioral interaction between northern bobwhite (*Colinus virginianus;* e.g., nest placement) and their predators (e.g., search methods for food acquisition). In order to understand habitat characteristics influencing predation, we studied bobwhite nests using 24-hour near-infrared video cameras. We monitored 675 bobwhite nests with cameras on 3 properties in northern Florida and southern Georgia, USA, during 2000–2006. To test the association between nest failures and specific failure causes with landscape structure, we calculated a suite of landscape metrics and examined these at 3 spatial scales (3.1 ha, 19.6 ha, and 50.3 ha). We found increased probability of nest success with greater proportions of, and proximity to, fallow and annually disked fields at larger scales (50.3 ha), but we found no landscape metrics to be important predictors of bobwhite nest failures at small scales (<20 ha). Fallow and disked fields may provide alternative prey items (e.g., rodents) important in buffering nest predation. Relative to meso-mammal predation, we observed increases in proportion of the landscape in field to be related to lower incidental nest failures at the smallest scale (3.1 ha). Nests closer to feed lines were more likely depredated by meso-mammals than ants at the 2 larger spatial scales. Interestingly, the fate of a nest was independent of the fate of neighboring nests, suggesting bobwhite nest predation may be primarily incidental.

Predation is a process that relies on the interactions among predators, prey, and the habitat where they coexist. Nest predation is considered the leading cause of nest failure for most avian species (Ricklefs 1969). Effective management to enhance breeding success of an avian species requires accurate identification of the predators responsible for failures, as well as knowledge of predator and prey distribution, abundance, diversity, and habitat use. Nest predation is likely to be in part the result of incidental encounters of predators with nests (Vickery et al. 1992, Jones et al. 2004). Therefore, management that reduces the probability of these interactions may result in

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increased reproductive success. Frequently, predator control is used to mitigate nest losses for many gamebirds and imperiled bird species; however, many conflicting results exist about its effectiveness to enhance avian reproductive success and abundance (Côté and Sutherland 1997, Newton 1998). Northern bobwhites (*Colinus virginianus*) are a declining grassland- and early successional-dependent species. Bobwhites are vulnerable to predation because they nest on the ground with large clutches and relatively long nest-exposure periods. Habitat management has been considered an effective tool at enhancing bobwhite populations based on the premise that predator populations can be manipulated indirectly through habitat modifications (Errington 1934, Rollins and Carroll 2001). This nonlethal method has been suggested as the first tool that should be implemented to offset predation losses (Rollins and Carroll 2001). In order to increase bobwhite reproductive output, biologists need to first understand the complex relationship among the predators, bobwhite nests, and the habitats, which leads to increased interactions between the nests and the predators.

Although nest success in northern bobwhites is well-studied, much less is understood linking predation and specific nest failures with habitat associations (Staller et al. 2002), and specifically what spatial scales might be most important to bobwhite reproductive success (Roseberry and Klimstra 1984, Taylor et al. 1999b, White et al. 2005). Radiotelemetry technology has enhanced our understanding of bobwhite nest selection; yet identification of the predators responsible for nest predation events is rarely known because signs at the nest may be misleading (Lariviere 1999, Staller et al. 2005, Lusk et al. 2006). Traditional studies of bobwhite nesting relative to habitat features have focused its influence on nest site selection or nest success (Taylor et al. 1999a, b; White et al. 2005; Collins et al. 2009). Only one study to date has examined the specific predator species responsible for bobwhite nest failures and their interactions with habitat characteristics (Staller et al. 2002). Advances in camera technology have enabled biologists to accurately identify nest predators and has become a popular tool in studying avian nest predation (Pietz and Granfors 2000, Staller et al. 2005). This technology can assist in identifying nest predators and might help link nest predation to habitat associations across the landscape.

Common bobwhite nest predators include raccoons (*Procyon lotor*), nine-banded armadillos (*Dasypus novemcinctus*), opossums (*Didelphis marsupialis*), bobcats (*Lynx rufus*), red and gray fox (*Vulpes vulpes* and *Urocyon cinereoargenteus*), coyotes (*Canis latrans*), skunks (*Mephitis mephitis*), snakes (*Elaphe* spp. and *Lampropeltis getula*), and fire ants (*Solenopsis* spp.; Hernandez et al. 1997, Fies and Puckett 2000, Staller et al. 2005). These predators have broad diet and habitat needs and they are thought to opportunistically feed on nests. Therefore, understanding how features on the landscape determine predator behaviors, such as foraging, has substantial value in managing not just bobwhites, but also grassland wildlife (Kuehl and Clark 2002).

Habitat edges may serve as travel corridors for many wildlife species, particularly medium-sized mammals (Heske et al. 1999, Chalfoun et al. 2002, Kuehl and Clark 2002, Phillips et al. 2003). However, some studies contradict the role linear edges may play in mammalian predator movement (Pasitschniak-Arts et al. 1998). Ecotones and other edges are frequently found to be preferred for snake species, particularly in northern regions (Weatherhead and Charland 1985). Edges may be important to predators, particularly where habitat patches are small with relatively little "core" area to be searched (Temple 1986). For some species, such as fox, activity is greater in smaller patches (Sovada et al. 2000) and is likely the result of a fragmented landscape with many edges that enable the predator to search the area with greater efficiency. Edges may attract avian nesting but these abrupt transition zones may serve as ecological traps where birds are more vulnerable to predation because of surrounding, low quality habitat.

Although many bobwhite predators are generalists, research is lacking on the habitat composition and configuration preferences that might influence the ability of these predators to find avian nests (Phillips et al. 2003). These generalist meso-mammals frequently exploit a variety of habitats including mixed habitats with forested area, shrub land, old fields, agricultural areas, wetlands, and suburban areas (Reid et al. 2006). However, some meso-mammalian predators were found to prefer specific habitat cover types in the Prairie Pothole Region of North America (Phillips et al. 2003). In addition, edge use was dependent upon the types of surrounding land cover, with wetlands being more attractive edges for meso-mammals (Phillips et al. 2003). Snake species utilize a variety of habitats including wooded and shrub areas with both hardwood and pine forests and wetland edges. Within the snake community, used habitats often are different even among closely related species. For example, corn snakes (*Elaphe guttata*) most often use upland pine areas, whereas gray rat snakes (*Elaphe spiloides*) are most often found in hardwood drains (Stapleton 2005). Thus, wildlife managers could benefit in understanding whether specific habitat composition and configuration of land-cover types might increase predation risk to avian nests by certain predator guilds.

The objectives of this study were to determine the landscape composition and configuration features important to nest fate and the specific predators responsible for nest failures across 3 different spatial scales. This was conducted by coupling radiotelemetry, nest camera technology, Geographical Information Systems (GIS), and spatial analysis tools. The findings of this study provide insight on spatial scales at which the nest predation process is occurring, underlying spatial relationships to the predation process, and potential management that may minimize nest predation.

STUDY AREA

We studied bobwhite nesting at 3 sites in southern Georgia and northern Florida during 2000–2006. Tall

Timbers Research Station and Land Conservancy, Inc. (Leon County, FL; 84°13′35″W, 30°39′39″N) and Pebble Hill Plantation (Thomas and Grady County, GA; 84°5′48″W, 30°46′13″N) are located in Red Hills physiographic region are. Pinebloom Plantation (Baker County, GA; 31°24′42″N, 84°22′45″W) is located in the Upper Coastal Plain physiographic region. Detailed site description for the Red Hills sites can be found in Staller et al. (2005), and for Pinebloom in Sisson et al. (2000, 2009). Sites are dominated by loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*) with associated "old-field" ground cover vegetation and areas of longleaf pine (*P. palustris*) with associated wiregrass (*Aristida stricta*) ground cover. All 3 sites use frequent fire (1–3-yr rotations), disking, roller-chopping, and mowing to maintain an open, low-density pine forest structure. Hardwood drains, hammocks, fallow fields, and wetlands are interspersed across the landscape. On the greater landscape, the adjacent land to Pinebloom Plantation includes some row-crop agriculture predominantly for cotton and peanuts. Supplemental feeding of bobwhites occurred on all 3 properties. Every 2–3 weeks, sorghum was spread at a rate of approximately 6 bushels/1.6 km on specified trails (feed lines). In addition to supplemental feeding, nest predator reduction was occurring on sites in some years from 1 March to 30 September. No predator reduction occurred on either site in 2000, but in 2001–2003 predators were reduced on the eastern half of Pinebloom Plantation and at Pebble Hill Plantation while Tall Timbers Research Station and Pinebloom West did not receive any predator reduction. From 2004 to 2006, the predator reduction efforts were switched and Tall Timbers Research Station and Pinebloom West had predator reduction while the other 2 sites served as controls. Detailed information about predator removal can be found in Ellis-Felege et al. (2012).

METHODS

Bobwhite Nesting

On each study site, we captured bobwhites each year between January and April, 2000–2006, using baited funnel traps (Stoddard 1931). We classified captured bobwhites by age and sex, and fitted each with 6.5g (~4% body-weight) collar-style radiotransmitters (Staller et al. 2005). All trapping, handling, and marking followed approved protocols by the University of Georgia Institutional Animal Care and Use Committee permits A2004-10109-c1 and A3437-0. Using radiotelemetry homing techniques (White and Garrott 1990), we located bobwhites ≥5 days/week to monitor nesting behavior between 15 April and 1 October of each year. Bobwhites found in the same location on 2 consecutive days and did not have the mortality sensor activated were assumed nesting. We placed flagging near the nest site location so the nest could be relocated when the incubating bobwhite was off the nest. We recorded the nest location into a geodatabase using GIS and ArcGIS software (Environmental Systems Research Institute, Inc., Redlands, CA, USA). We were able to find nests and begin monitoring

within the first few days of incubation so nests were approximately the same age when located (Taylor et al. 1999b).

When the incubating bobwhite was away from the nest as determined by telemetry, we installed a continuous-recording, near-infrared camera (Furhman Diversified, Seabrook, TX, USA) at the nest. We placed the small camera with a near-infrared (950-nm) lighting source approximately 1–1.5 m from the nest opening (Staller et al. 2005). We camouflaged the cameras using surrounding vegetation. Cameras and lighting sources were linked via a 25-m cable to very high standard (VHS) recorders and 225-reserve capacity, deep-cycle battery. We modified the recorders to operate at one-third speed, allowing an 8-hour tape to last 24 hours. We replaced tapes and batteries daily. We checked nests daily via telemetry until failure or hatch, thus minimizing errors in failure dates. We viewed videos to confirm fate of the nest and identify the nest predator if the nest failed. We categorized nests first as successful (i.e., hatched ≥1 egg) or failed. From camera monitoring, we further classified failed nests as failed due to meso-mammals, snakes, ants, and other factors (e.g., incidental predators or bobwhites killed away from the nest). We did not explore predation patterns relative to partial clutch loss and individual egg mortality but rather only those where no eggs hatched from a nest.

Land Cover

We digitized land-cover types at 1:1,500-m scale using 1999 Digital Orthophoto Quarter Quadrangles in ARCMAP v9.2 (Environmental Systems Research Institute, Inc.). To validate land-cover types and to update polygons for the study years (2000–2006), we used first-hand knowledge of the study area, remote imagery, and handheld GPS locations from the field. We delineated 10 land-cover types. These included pine (i.e., open pine savannah), planted pine (i.e., densely planted pine stands), agriculture (i.e., row crops), ragweed and fallow fields, hardwood drains, roads, feed lines, wetland, open water, other (i.e., predominantly urban).

Landscape Metrics

We were most interested in spatial relationships of nest fates relative to the composition of the landscape at different scales, proximity of specific landscape features to the nest, and amount of edge near nests at the different scales. We constructed circular buffers around each nest site with radii of 100 m (3.14 ha), 250 m (19.6 ha), and 400 m (50.3 ha). We selected buffer sizes based upon the variety of home range sizes in the predator community with home ranges <20 ha for armadillos and snakes (Layne and Glover 1977, Stapleton 2005), approximately ≥50 ha for raccoons (Chamberlain et al. 2003a) and at the site-level spatial scale for bobcats and coyotes (Chamberlain et al. 2003b). We chose not to use larger radii because of substantial overlap among nests that would have resulted in nonindependence in our data and required us to remove nearby nests, thus decreasing sample sizes.

These scales encompassed bobwhite home ranges on the study areas (Sisson et al. 2000, Wellendorf and Palmer 2009), were representative of home ranges in other areas of Georgia (Parnell et al. 2001), and were comparable to previous studies examining bobwhite nesting relative to landscape characteristics (Staller et al. 2002, White et al. 2005). We intersected each buffer size with the land-cover layer of the study areas using ARCMAP intersect tools. Within each buffer, we calculated percent composition of the habitat cover types. We calculated Euclidean distance between nests to landscape features of interest (e.g., roads, feedlines, hardwood drains). Using FRAGSTATS (Version 3.3; McGarigal et al. 2002), we used a moving-window analysis to calculate edge density at each scale (total length of edge in the landscape divided by total area of landscape and did not include edges from perimeter of the buffer). We focused on edge density because edges are thought to be primary travel corridors for predators. We extracted these values to the nest point using the Spatial Analyst Tool "Extract Values to Point" in ARCMAP.

Statistical Analysis

First, we assessed nest failures (e.g., success or fail) relative to specific landscape metrics using a logistic regression in SAS (Version 9.3; SAS Institute, Inc., Cary, NC, USA). We initially examined models at each of the 3 spatial scales to determine which models were most important at the individual scales. To avoid collinearity, we conducted Pearson correlations on all pairs of predictor variables. We considered $r^2 > 0.3$ to be a conservative estimate of correlated variables (Moore and McCabe 1993) and thus did not use them in the same regression model. We selected one of the metrics we hypothesized might be most important in the interaction of predators with the nest. We selected 9 metrics to use as predictors variables including percent of hardwood composition within each buffer, percent of wetland composition within each buffer, percent of annually disked fields composition within each buffer, edge density at each buffer size, distance to hardwoods, distance to fields, distance to wetlands, distance to roads, and distance to feed lines. Rather than run all combinations of models, we explored *a priori* models of individual parameters of interest, combinations of models that we thought were biologically important, and a global model (all uncorrelated parameters of interest). Biologically important combinations included models about both distance to and composition size to a particular habitat type (specifically, wetland or hardwood drain habitats), additive model of distance metrics to all features of interest given the importance to edges, and composition-only models that include overall composition of fields, wetlands, and hardwood drains. We examined $\hat{c}$ of the global model to determine whether the data were over-dispersed where a $\hat{c} > 1.0$ represents overdispersion (Lebreton et al. 1992). We ran a Hosmer–Lemeshow goodness-of-fit test in SAS on the global model, where an adequate fit is observed if the $P > 0.05$ (Hosmer and Lemeshow 1989). We found no overdispersion, so we used model selection approaches (Akaike's Information

Criterion adjusted for small sample sizes; AIC_c) to determine the models that described the data best (Burnham and Anderson 2002). The best-fitting models at each scale and a global model of scale-independent metrics were then used in a subsequent multiscale analysis to determine which scale, if any, described the probability of nest failures best. Model-averaged estimates from the entire candidate model set were calculated for the coefficients of the predictor variables (Burnham and Anderson 2002, Anderson 2008). Model-averaged odds ratios were calculated for the parameter estimates and for interpretation, scaled to biologically significant values important for management at each of the 3 spatial scales and for a multiscale model using the top 2 models from each individual scale.

Second, conditioned on nest failure, we examined the specific cause of nest failure (e.g., meso-mammal [baseline], snake, ants, and other) relative to landscape metrics using a multinomial model at the 3 spatial scales. We selected uncorrelated metrics as described above in the nest success models, and evaluated goodness-of-fit using a likelihood ratio test, where adequate fit is observed if $P > 0.05$ (Menard 2002). Models were evaluated at each of the 3 spatial scales using AIC_c model-selection approaches described above for the logistic models (Burnham and Anderson 2002). We present model-averaged estimates for each of the coefficients of the predictor variables with odds ratios scaled to biologically relevant values important to management for interpretation and provide summary information for the parameters in the top models.

Additionally, we examined the residuals of the top regression models and calculated Moran's I to determine if any spatial structure was not accounted for by the predictor variables (Overmars et al. 2003) using Program SPATIAL ANALYSIS in Macroecology (SAM; version 3.1, http://www.ecoevol.ufg.br/sam/; Rangel et al. 2006). We also explored spatial structure within our response variables by plotting correlograms and examining average Moran's I to determine whether any spatial structure might exist in the underlying nest failure process. A Moran's I-value near 0 indicates no spatial autocorrelation where values near 1 and -1 indicate clustering and randomness, respectively (Cliff and Ord 1981).

RESULTS

During the 7-year study, cameras were installed at 675 bobwhite nests (Felege 2010). We excluded 29 nests from subsequent analysis because these nests were abandoned as a result of research activities (primarily a result of camera installation). Of the remaining 646 nests, 394 nests (61.0%) succeeded and 252 (39.0%) failed. We examined ultimate causes of nest failure and not individual egg mortality or any partial predation events. The specific failures were attributed to meso-mammals ($n = 92$ nests: 36.5% of failures), snakes ($n = 67$ nests: 26.6% of failures), ants ($n = 28$ nests: 11.1% of failures), and other incidental causes ($n = 30$: 11.9% of failed nests). At 35 nests (13.9% of failed nests), exact failure causes could

Table 1.   Model selection using Akaike's Information Criterion (AIC_c) weights of the top 2 models from each of the 3 spatial scales and a global model of uncorrelated metrics incorporated into a multiscale model examining the relationship between the probability of northern bobwhite nest failure and landscape metrics in northern Florida and southern Georgia, USA, 2000–2006. For the smaller scales, the models were both scale-independent metrics for proximity and the same models described the data best.

Model	K	AIC_c	ΔAIC_c	Weight
Int + Field Distance + Field Composition (50.3 ha)	3	914.52	0.00	0.352
Int + Field distance + Field Composition (50.3 ha) + Wetland Distance + Hardwood Distance	5	915.03	0.50	0.274
Int + Hardwood Distance	2	915.05	0.53	0.270
Int + Wetland Distance + Hardwood Distance	3	916.96	2.44	0.104

not be determined from the camera footage because dense vegetation often limited visibility for small species (e.g., snakes). Failures classified as unknowns were not meso-mammals predators because these predators were easily identified even in thick vegetation but were suspected to be snakes (Staller et al. 2005). Unknown failures were included in the logistic failure models only. More detailed descriptions of annual and by study area nest failures can be found in Ellis-Felege et al. (2012).

Nest Failures Relative to Landscape Features

Global models at all scales demonstrated adequate fit ($P > 0.05$) and no overdispersion was observed in the data ($\hat{c} = 1.01$). The best-fitting models included distance to hardwood drains only and an additive model of distance to hardwoods and to fields for both the 3.1-ha and the 19.6-ha models. However, no predictors strongly influenced the probability of nest failures at the 2 smaller scales (3.1-ha and 19.6-ha scales). Model-averaged parameter estimates for these predictors had estimates close to 0 and 95% confidence intervals encompassing 0 with no strong trend for a positive or negative relationship with nest failures. At the 50.3-ha scale, the best-fitting model describing the probability of nest failures was percent field composition and distance to fields ($AIC_w = 0.455$). Within the 50.3-ha buffered area, the probability of nest failure was 1.6 times less likely with each 10% increase in field composition. Probability of nest failure was 1.1 times less likely with each 50-m increase in distance between the nest and the field.

The top 2 models at each scale, and the global model, were then examined as a candidate model set to determine which scale best described the probability of failure. The top model was an additive model of percent field composition at the 50.3-ha scale and distance to fields (Table 1). This model had 40.5% of the model weight and was 1.3 times more likely than the next best-fitting model

of distance to hardwood patches. At the 50.3-ha scale, the probability of nest failure was 1.7 less likely with every 10% increase in field composition (Table 2). For every 50-m increase in proximity to fields, the probability of nest failure was 1.1 times less likely (Table 2). Successful nests, on average, were farther from field edges and wetlands, but closer to hardwood drains (Table 3).

We found no spatial autocorrelation in the residuals of the overall top model for the probability of nest failure (Moran's $I_{avg} = -0.008$; Fig. 1); therefore, no modification to the modeling structure was necessary (Cliff and Ord 1981). We examined the correlogram for the response variable of nest success or failure with respect to the proximity of nests from one another and found overall no spatial pattern (Moran's $I_{avg} = -0.009$). We hypothesized that predation at neighboring nests would be more likely related to nests within the same year so we further examined the spatial relationship of the response variable by year. Generally, we found very little spatial relationship in nest fate relative to the nest fate of neighboring nests (Fig. 2), except for 2002 and 2005 where there appeared to be slight clustering in the fate of nests within 200 m of one another (Moran's $I = 0.36$ and 0.42, respectively).

Specific Failure Causes Relative to Landscape Features

Global models at each scale indicated adequate fit for the multinomial models examining landscape metrics on specific failure causes ($P > 0.05$). Predator-specific failure causes were influenced differently by landscape metrics at the 3.1-ha scale compared with the 2 larger scales. Distance to fields was in top models at all 3 scales. Percentage of fields described the data best at the 3.1-ha and 19.6-ha scales, whereas the best-fitting models included percentage of hardwoods. Most of the model-averaged parameter estimates were near 0 and had broad

Table 2.   Model-averaged parameter estimates for coefficients of the landscape metrics potentially influencing the probability of northern bobwhite nest failures in northern Florida and southern Georgia, USA, 2000–2006.

| Parameter	Estimate	SE	95% LCI	95% UCI	Unit scalar	Scaled odds ratio	Scaled LCI	95% CI UCI
Intercept	−0.0481	0.40251	−0.837	0.6121				
Distance to fields	−0.0021	0.00094	−0.004	−0.0006	50	0.8998	0.8208	0.9719
Field composition (50.3 ha)	−0.0488	0.01917	−0.0864	−0.0174	10	0.6138	0.4215	0.8405
Distance to wetlands	−0.0001	0.00028	−0.0007	0.0003	50	0.9936	0.9666	1.0166
Distance to hardwoods	0.0004	0.00018	0	0.0007	50	1.0181	1.0000	1.0336
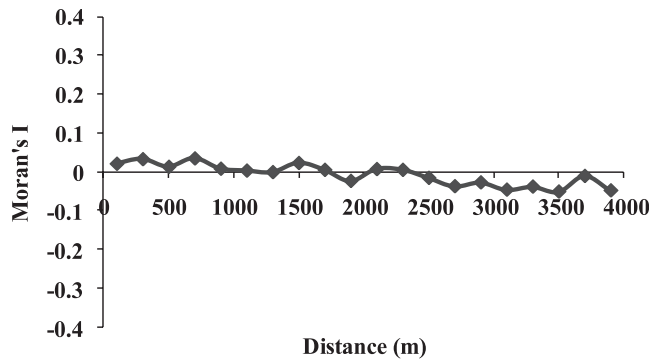
Fig. 1. Correlogram of Moran's *I* for the spatial structure of the residuals of the top model (Percent Field Composition at 50.3-ha scale + Distance to Fields) for the probability of northern bobwhite nest failure during 2000–2006 in southern Georgia and northern Florida, USA. Values of Moran's *I* close to 0 indicate no spatial autocorrelation.

95% confidence intervals that encompassed 0. When we examined models from each spatial scale, we found the smallest scale predictor of percentage of field composition best described the probability of predator-specific failure (Table 4). At the 3.1-ha scale, for every 10% increase in field composition, other predation events were 2.2 times less likely than meso-mammal predation events (Table 5). On average, higher proportions of field within the smallest scale buffer were associated with ant predation (Table 6). With every 10% increase in field composition, we found ant predation to be 1.3 times more likely than meso-mammal predation events and snake predation events to be 1.1 times more likely than meso-mammal events at the smallest scale (Table 5). For every 50-m increase in proximity to feed lines, ant depredations were 1.04 times more likely than meso-mammal predation events (Table 5). Meaning, on average, most meso-mammal predation events were closer to feed lines than any other nest failures (Table 6). We also found that each 10% increase in hardwood composition at the 50.3-ha scale increased the probability of ant predation by 1.3 times that of meso-mammals (Table 5).

We examined spatial structure in the response variable by comparing meso-mammals first with all other failure causes collectively (i.e., snakes, ants, and other). Then, we compared meso-mammals with each of the other 3 failure causes individually. Similar to the success–failure model, we observed little spatial autocorrelations among the nest failure cause of neighboring nests when meso-mammals were compared with all other failure causes collectively or individually (Moran's $I_{avg} < 0.2$).

DISCUSSION

We found that the relationship between fate of bobwhite nests and landscape attributes was dependent upon the spatial scale at which the landscape metrics were evaluated. At the small scale (<20 ha), metrics were not particularly informative for explaining nest fate and models best describing the failure process were scale-independent metrics of proximity. Failures at nests can result from a large suite of different predator species, each with their own foraging methods and relationship with the habitat features we explored. These smaller scales correspond to some of the predominant predator species, such as armadillos (Layne and Glover 1977) and gray rat snakes (Stapleton 2005), which have home ranges <20 ha. However, many of the predators, such as raccoons (Urban 1970, Chamberlain et al. 2003a), have large home ranges that exceed 20 ha. In fact, top predators such as bobcats and coyotes have home ranges that can exceed even our largest scale (Chamberlain et al. 2003b).

At larger scales (>50 ha), we found the greater the percent field composition the more likely the nest was to succeed. Our results suggest that the nest predation process is likely operating at scales related to the larger predator home-range sizes. Annually disked fields, ragweed fields, and fallow fields provide sources of food to bobwhites that would be valuable during the nesting season (Klimstra and Roseberry 1975). Having these habitats readily available may minimize bobwhite foraging time or number of daily foraging trips that may leave a nest more vulnerable to predation. Perhaps more importantly, though, is the role of cotton rats (*Sigmodon hispidus*). Cotton rats are a common alternative prey item for many bobwhite predators (Schoch 2003) and work done on our study area demonstrated fields are preferred habitat for this species at our study sites (Hannon 2006). Thus, a greater abundance of cotton rats might equate to a greater abundance of alternative prey options for predators. Nesting studies examining alternative prey have found increased availability of alternative prey to be correlated with greater nesting success for waterfowl (Byers 1974, Weller 1979, Crabtree and Wolfe 1988, Vander Lee et al. 1999). Although this might be directly related to alternative prey availability, this might also be a function of diversion of predators to habitats for foraging where bobwhites do not commonly nest. Potentially there is an interactive effect of alternative prey and foraging diversion.

Examining predator-specific failures, we found that at the smallest scale (3.1 ha) field composition was also important. At the smallest scale, percent field composition

Table 3. Summary statistics of landscape metrics in top models relative to successful and depredated bobwhite nests in northern Florida and southern Georgia, USA, 2000–2006.

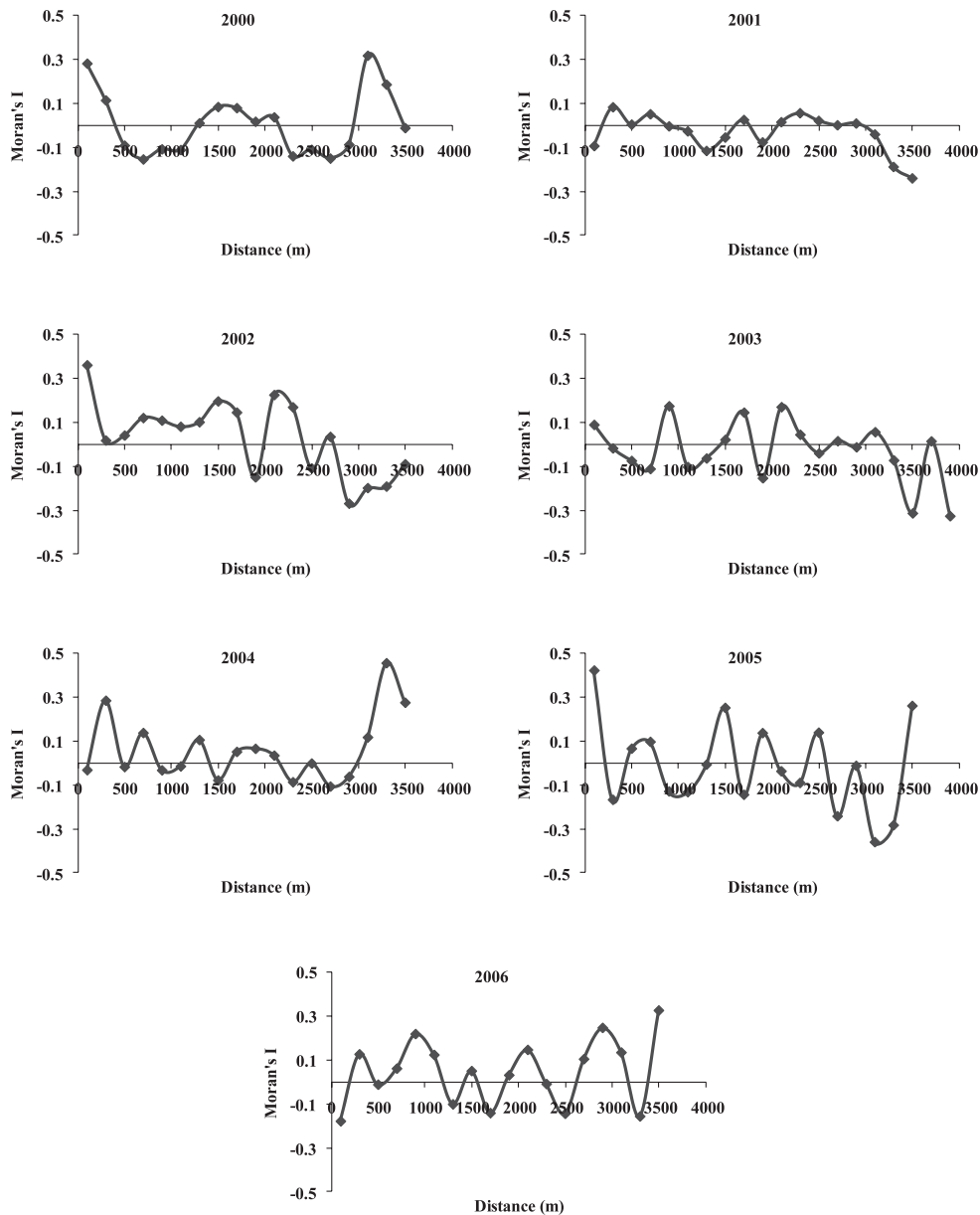| Nest fate	Distance to field (m)			% Field composition (50.3 ha)			Distance to wetland (m)			Distance to hardwood drain (m)		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Success	122.51	0.00	473.84	7.04	0.00	24.45	417.88	0.00	1,701.07	329.99	0.00	2,442.16
Fail	112.43	0.00	470.06	6.29	0.00	21.96	389.41	0.00	1,364.57	439.72	0.00	2,174.38

Fig. 2. Correlogram of Moran's *I* for the binary response variable of success or failure of northern bobwhite nests during 2000–2006 in southern Georgia and northern Florida, USA, showing the spatial autocorrelation between nests, where *I*-values close to 0 indicate no relationship in nest fate to the fate of neighboring nests.

described the data best for incidental failures compared with meso-mammals predation events at the nest. Many of the incidental failure causes were the result of mortality of the incubating bobwhite while it was away from the nest. From a management perspective, there is still the potential for renesting when the nest fails because of predation by meso-mammals as long as the bobwhite survives.

Distance to feed lines was important in ant depredations relative to meso-mammals at the 2 larger scales. There is relatively little understood about the how fire ants interact with habitat management. Habitat disturbances such as burning and mowing appear to enhance ant populations (Williamson et al. 2002) but supplemental feeding practices have not been examined relative to ants.

The red imported fire ants could be attracted to seeds and are known to disperse seeds of native plant species (Zettler et al. 2001, Stuble et al. 2009); however, we found on average most ant predation events were farther from feed lines than other predators. Other studies have documented trends that supplemental feed lines attract bobcats (Godbois et al. 2004) and avian predators (Haines et al. 2004) and may be playing a role in our findings.

We observed no differences between landscape features that strongly influence snake predation differently from meso-mammals. Only percent field composition appeared to slightly increase snake predation relative to meso-mammals at our smallest scale, but decreased snake predation relative to meso-mammals at the 19.6-ha scale.

Table 4. Model selection using Akaike's Information Criterion (AIC$_c$) weights of the top 2 models from each of the 4 spatial scales incorporated into a multiscale model examining the relationship between the probability of specific failure causes (meso-mammals, snakes, ants, and other) at northern bobwhite nests and landscape metrics in northern Florida and southern Georgia, USA, 2000–2006. Scale-independent metrics for proximity to feed lines described the predator-specific failure causes best at the 2 larger spatial scales (19.6 ha and 50.3 ha).

Model	AIC$_c$	ΔAIC$_c$	Weight
Int + Field composition (3.1 ha)	549.75	0.00	0.700
Int + Field composition (3.1 ha) + Feed line distance	551.97	2.22	0.231
Int + Feed line distance	556.30	6.55	0.026
Int + Field composition (19.6 ha)	556.57	6.82	0.023
Int + Hardwood composition (50.3 ha)	556.91	7.16	0.019

These predator guilds are generalists and have very broad habitat and diet requirements as well as potentially species-specific habitat preferences. By pooling snakes into one category, we may have obscured habitat characteristics influential to specific snake species. For example, gray rat snakes in the area of this study frequently used hardwoods and wetlands more than corn snakes, which predominantly used upland pine habitat (Stapleton 2005). Furthermore, kingsnakes may be more likely found in the uplands than rat snakes (Ernst and Ernst 2003). Staller et al. (2002) recommended bobwhite nesting cover be promoted away from drain edges to reduce snake predation but gray rat snakes were the predominant snake species in that study. However, in our study, this would only partially mitigate snake predation. On one of our study sites, Pinebloom, kingsnakes were the primary snake predators, whereas both species of rat snakes were the common snake predators in the Red Hills Region. Unfortunately, it was not always possible to identify snakes to species from our camera data. Thus, future work focusing on species-specific failures may yet identify habitats or landscape structures related to increased risk of failure.

We observed that fate of an individual nest appeared to be spatially independent of the fate of neighboring nests during most years. Although it may seem intuitive that predators would return to an area where they previously had success, research on learning and foraging theory suggests otherwise (Real 1994). For example, this could be the result of predators selecting among patches with varying resource availability. An alternative explanation could be that predators are trying to search an area efficiently; therefore, they might not return to an area previously exploited because they have already searched it. Angelstam (1986) also found predators did not appear to develop a memory for the location of artificial nests. For generalist predators like those in our study, it may be that random foraging modified by some selection of habitats with large amounts of alternative food sources, such as fields, is the most efficient search method because predators have broad dietary requirements that can easily be met within this landscape. Thus, predation on bobwhite nests is probably incidental, as has been found for other grassland bird nests functioning as incidental prey for striped skunk (Vickery et al. 1992).

Years (2002, 2005) for which we observed a slight spatial pattern in the nest fate were years when production was very high, and many bobwhites on our study areas had second nests. We observed renests by individual birds to be fairly close to one another. Thus, the relationship between proximity and nest fate may have been less an artifact of the predation process but instead related to the success of an individual bird. In other words, bobwhites

Table 5. Model-averaged parameter estimates for the coefficients of landscape metrics influencing the probability of northern bobwhite nest failures due to specific predators (meso-mammals, snakes, ants, and other failures) in northern Florida and southern Georgia, USA, 2000–2006.

Parameter	Estimate	SE	LCI	UCI	Unit scalar	Scaled odds ratio	Scaled LCI	95% UCI
Intercept[a]	−0.787	0.270	−1.317	−0.257				
Intercept[b]	−1.502	0.317	−2.124	−0.881				
Intercept[c]	−0.396	0.211	−0.810	0.018				
Field composition (3.1 ha)[a]	−0.077	0.037	−0.150	−0.005	10	0.462	0.224	0.953
Field composition (3.1 ha)[b]	0.026	0.019	−0.010	0.063	10	1.302	0.905	1.874
Field composition (3.1 ha)[c]	0.010	0.015	−0.020	0.040	10	1.105	0.817	1.493
Feedline distance[a]	0.000	0.000	−0.001	0.001	50	1.002	0.959	1.047
Feedline distance[b]	0.001	0.000	0.000	0.001	50	1.036	0.999	1.073
Feedline distance[c]	0.000	0.000	0.000	0.000	50	1.001	0.999	1.004
Field composition (19.6 ha)[a]	−0.058	0.040	−0.137	0.021	10	0.559	0.254	1.232
Field composition (19.6 ha)[b]	0.028	0.032	−0.035	0.091	10	1.323	0.708	2.473
Field composition (19.6 ha)[c]	−0.018	0.027	−0.070	0.035	10	0.839	0.497	1.417
Hardwood composition (50.3 ha)[a]	−0.003	0.020	−0.042	0.036	10	0.967	0.654	1.428
Hardwood composition (50.3 ha)[b]	0.030	0.017	−0.004	0.063	10	1.343	0.961	1.878
Hardwood composition (50.3 ha)[c]	−0.005	0.015	−0.034	0.025	10	0.955	0.709	1.286

[a] Other nest failure causes relative to meso-mammals depredations.
[b] Nest failures due to ants relative to meso-mammals depredations.
[c] Nest failures due to snakes relative to meso-mammal depredations.

Table 6.   Mean and range of landscape metrics at bobwhite nests delineated by nest failure cause and successful nests in northern Florida and southern Georgia, USA, 2000–2006.

Nest fate	% Field composition (3.1 ha)			% Field composition (19.6 ha)			R Hardwood composition (50.3 ha)			Distance to feed line (m)		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Meso-mammal	7.15	0.00	53.48	6.75	0.00	26.84	8.46	0.00	53.04	373.70	0.00	1,999.04
Snake	8.24	0.00	42.94	6.10	0.00	22.03	7.94	0.00	44.41	403.05	0.00	1,510.99
Ant	10.62	0.00	39.87	7.98	0.00	27.45	12.86	0.00	39.25	624.26	0.00	2,043.01
Other	2.91	0.00	19.81	4.90	0.00	29.18	8.08	0.00	36.94	388.05	0.77	1,909.00
Successful	6.86	0.00	80.97	7.21	0.00	37.00	9.54	0.00	55.28	414.13	0.00	2,101.86

with successful first nests were more likely to have successful second nests or vice versa. Microhabitat features selected by the bobwhite may have influenced the fate of the nest. Amount of litter cover, vegetation height, and presence of specific plant species may camouflage some nests better than others (Taylor et al. 1999a) and certain bobwhites might be better at microhabitat selection for nest sites than are other bobwhites.

Studies have found edges to be important (Heske et al. 1999, Chalfoun et al. 2002, Kuehl and Clark 2002, Phillips et al. 2003) but we did not find edge density or distance to edges to strongly influence the probability of nest failures except for field edges. Although models at smaller scales indicated distance to edges of hardwoods described the data best from our model-selection approaches, this predictor was no more or less likely to influence nest fate. Distance to field edge, however, was negatively related to the success of a nest and may have been related to attributes of the field that attracted predators to these sources of abundant alternative prey. Therefore, increased probability of nest encounter by a predator would be more likely. These results seem to contradict our findings of increased field composition benefiting bobwhite nesting. There is a definite tradeoff but, in most cases, the percentage of these fallow or annually disked ragweed fields on the larger landscapes is generally small. For example, our observed ranges were 0–25% field composition at the 50.3-ha scale.

The impact of cameras at nests is always a concern for interpretations of nest predation and bird behaviors. Work by Staller et al. (2005) on a subset of the bobwhite nesting data presented here found no impacts of cameras on nesting birds. However, because it is difficult to determine predator fates without cameras (Pietz and Gransfors 2000, Staller et al. 2005, Rader et al. 2007) and whether specific predators may be attracted or deterred by the camera setups, it is largely unknown what specific impacts, if any, the cameras may have on predator-nesting bird interactions. Thus, our interpretations are based upon the predators we observed at the nests from the cameras and may have unknown biases.

MANAGEMENT IMPLICATIONS

Our results suggest that creation of early succession-al, fallow fields, which is often done to create bobwhite brood habitat, also benefits nesting and therefore should be encouraged. It is important to note that our maximum field composition was 25% and therefore model results should not be extrapolated to landscapes composed of higher fractions of field habitat. Our results also suggest that feed lines along roads might impact nesting bobwhites by creating additional food resources for mammals or attracting mammals to those areas. The tradeoff in management is likely to be in the timing of when managers stop providing feed after winter.

One caveat of our study is that we monitored bobwhites in a habitat that is managed to sustain high bobwhite densities; therefore, influences of many potential factors that could drive the predation process may have been diluted relative to their effects in more degraded habitats typical of the modern landscape. Future work should focus on extending our study toward understanding predation in areas with intensive agriculture, forestry, and more fragmented habitats. A better understanding of landscape-mediated predation pressure in these areas may offer additional management alternatives for biologists to minimize predator–bobwhite interactions during the breeding season.

ACKNOWLEDGMENTS

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