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Research Article

Landscape Heterogeneity Reduces Coyote Predation on White-Tailed Deer Fawns

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ABSTRACT Coyote (*Canis latrans*) predation on white-tailed deer (*Odocoileus virginianus*) fawns in southeastern North America has led to deer population declines in some areas. Research or management efforts initiated in response to coyote predation on fawns have primarily focused on implementation of reduced antlerless deer harvest or coyote control to mitigate population declines. Vegetation characteristics may influence coyote hunting efficiency, but the potential influence of land cover at large scales in the southeastern United States is underexplored. We investigated whether mortality risk was affected by landscape characteristics within fawn home ranges for a sample of 165 fawns on the United States Department of Energy's Savannah River Site (SRS), South Carolina, 2007–2012. We monitored fawns every 8 hours to ≥4 weeks of age and 1–3 times daily to 12 weeks of age. We included only surviving or coyote-predated fawns in the dataset. The most supported model describing hazard ratios included the length of edge (i.e., area where 2 land cover types joined) in fawn home ranges. Probability of coyote predation increased 1.26 times for each 968-m decrease in edge within a fawn's simulated home range (29.1-ha circular buffer) under this model. Further, fawns with the least edge in their home ranges were >2 times more likely to be depredated by a coyote than fawns with the greatest edge availability. Support for other models was relatively low, but informative variables (e.g., mean patch fractal dimension, Shannon's diversity index, mean forest patch size) supported a general trend that as fawn home ranges became more homogeneous and contained larger patches with less edge and fewer cover types, predation risk increased. These findings are consistent with similar work in the midwestern United States, despite landscape differences between regions. The combined weight of evidence suggests maintenance of a heterogeneous landscape consisting of relatively small dispersed patches may reduce fawn losses to coyotes. This information may also be used to identify areas susceptible to greater fawn predation rates across large spatial scales. However, the relatively long forestry rotation lengths and large scale of consistent forest management on the SRS are uncommon in the southeastern United States and the mechanism for the pattern we observed is unclear. Therefore, our results may not be applicable to sites with different forest management practices. © 2017 The Wildlife Society.

KEY WORDS *Canis latrans*, coyote, fawn, habitat, *Odocoileus virginianus*, predation, survival, white-tailed deer.

A growing body of literature suggests coyote (*Canis latrans*) predation can significantly reduce white-tailed deer (*Odocoileus virginianus*) fawn survival or recruitment in parts of southeastern North America (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015*b*, Nelson et al. 2015). Given the significant value of whitetails as a game species, researchers and managers have considered or implemented a variety of management actions intended to mitigate fawn losses to coyotes. The most obvious example is coyote control. Early studies suggested lethal removal of coyotes was an effective measure, significantly increasing fawn recruitment in Georgia, Alabama, and Texas (Beasom 1974, Howze et al. 2009, VanGilder et al. 2009). However, results from more recent multi-year studies suggest the outcome of coyote control is more ambiguous. In South Carolina, 3 years of intensive coyote removal had only a modest positive effect on fawn survival (Kilgo et al. 2014). Similarly, the effects of coyote removal on coyote abundance and fawn recruitment varied spatially and temporally in Georgia (Gulsby et al. 2015). Even in cases where coyote control benefits deer populations, the rapid influx of transient coyotes likely necessitates repeated, intensive removal efforts (Gulsby et al. 2015, Hickman et al. 2015).

State wildlife agencies generally lack the resources to implement statewide coyote control programs, especially given the uncertain outcome of such efforts. Instead, several Southeastern states (e.g., Alabama, Georgia, South Carolina)

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have reduced or are considering reduction of bag limits on antlerless deer. This decision is supported by population models that indicate increasing adult female survival through reduction or elimination of antlerless harvest is sufficient to stabilize deer populations, except in extreme instances of low adult female survival and recruitment (Robinson et al. 2014). However, even complete protection of adult females from harvest may not offset population declines when predation rates on fawns are high and deer density is low because adult female survival may already be high (Kilgo et al. 2016), leading to additional management actions such as coyote removal (Chitwood et al. 2015*a*).

Frequently, deer managers implement coyote removal with the objective of increasing fawn survival by decreasing the number of coyotes within the area of concern. Presumably, this has no effect on the rate at which remaining coyotes depredate fawns. In contrast, factors that potentially do affect this rate include landscape composition and the net profitability of fawns as a food item. Coyote foraging efficiency varies with landscape composition (Gese et al. 1996, Richer et al. 2002, Rohm et al. 2007, Grovenburg et al. 2012), and in landscapes where the ability of coyotes to locate and capture fawns is diminished, the incentive to target fawns as a primary food item may be reduced (Rohm et al. 2007). More generally, optimal foragers should cease foraging on a specific food item when the energetic costs of foraging for that item under certain conditions exceed the benefits derived from the activity (Brown 1988).

However, the role of landscape composition in coyote predation on fawns in the Southeast is relatively unexplored, with recent literature focusing only on visual obstruction, or vegetation characteristics within the immediate vicinity of fawns. For example, Kilgo et al. (2014) examined the relationship between fawn survival and visual obstruction within fawn home ranges in South Carolina. Similarly, researchers in North Carolina evaluated the relationship between bedsite cover and fawn survival (Chitwood et al. 2015*b*). Neither study identified strong effects of microhabitat features on survival. However, predation is a complex process, influenced by cover conditions at multiple spatial scales (Brown and Litvaitis 1995), and the configuration of habitat patches on the landscape (Andrén 1995).

In contrast, researchers in the Midwest documented relationships between the size, shape, and arrangement of habitat patches and fawn survival in areas where coyotes were a significant source of fawn mortality (Rohm et al. 2007, Grovenburg et al. 2012). The results of these studies are a useful starting point in exploring the role of landscape composition and structure in coyote depredation of fawns in the Southeast, but landscape composition differs substantially between these regions. Therefore, our objective was to evaluate a series of hypotheses related to how the size, shape, and arrangement of land cover types within fawn home ranges influence predation risk for fawns in the Southeast.

Because previous work demonstrated visual obstruction or vegetation structure within fawn home ranges or at bedsites was not an important predictor of predation risk (Kilgo et al. 2014, Chitwood et al. 2015*b*), we predicted instead that predation risk would decrease as the area or density of patches with high visual obstruction increased. Also, predator–prey interactions are often related to edges between different types of habitat patches (Andrén 1995), and fawn survival may be greater in areas containing more edge (Rohm et al. 2007). Therefore, we predicted that fawn predation risk would decrease as edge in fawn home ranges increased. In contrast, we predicted that predation risk would increase as the area or average patch size of closed-canopy forests increased because closed-canopy forests offer limited cover near ground level. Finally, we predicted that predation risk would increase as home ranges (i.e., the landscape) became less diverse.

STUDY AREA

We conducted the study on the United States Department of Energy's Savannah River Site (SRS). The SRS is a 78,000-ha National Environmental Research park situated in the Upper Coastal Plain physiographic region of South Carolina. The SRS had a humid subtropical climate. Mean annual temperature was 18°C and mean annual rainfall totaled 122.5 cm. Summers were hot and humid, and winters relatively mild. Greatest rainfall occurred in March and July–August, whereas April and November were the driest months. Greater than 90% of the land area was under active forest management. Upland sites were dominated by loblolly pine (*Pinus taeda*) and longleaf pine (*Pinus palustris*) forests managed on 50–100 or 120-year rotations, respectively. The floodplains of the Savannah River and its major tributaries were dominated by bottomland hardwood and cypress (*Taxodium distichum*)-tupelo (*Nyssa aquatic* and *N. sylvatica* var. *biflora*) forests (Kilgo and Blake 2005). White-tailed deer and feral pigs (*Sus scrofa*) were the dominant large mammals, whereas coyotes and bobcats (*Lynx rufus*) were the dominant predators on the site.

Deer population density on SRS was low (4–8 deer/km^2). The SRS reduced deer harvest goals beginning in 2005 in response to a perceived decline in deer recruitment resulting from coyote predation on neonatal fawns. Coyotes were first documented at SRS in the mid-1980s, and density was estimated at 0.8–1.5 coyotes/km^2 at the beginning of the current study (Schrecengost 2007). Later research indicated fawn survival was 0.22 (95% CI $=$ 0.14–0.32) to 16 weeks of age, with coyotes potentially accounting for 80% of observed mortalities (Kilgo et al. 2012). Kilgo and Blake (2005) and Kilgo et al. (2010) provide more detail on deer and coyote management at SRS.

METHODS

We used survival and cause-specific fawn mortality datasets collected during 2007–2012 on the SRS and reported in Kilgo et al. (2012, 2014) to examine the influence of landscape and class characteristics on coyote predation on fawns. Briefly, they captured fawns with the aid of vaginal implant transmitters (VIT) placed in chemically immobilized females $\geq$1.5 years old during January–April 2007–2012. During the fawning season, they monitored VIT signals at 8-hour intervals. They initiated searches with thermal imaging cameras upon detection of an expelled VIT, after allowing for a ≥3-hour post-partum bonding period between the female and fawn. Researchers estimated ages of fawns captured opportunistically from unmarked females using new hoof growth (Sams et al. 1996). They equipped fawns with an expandable, breakaway radio-collar equipped with a motion-sensitive mortality switch on a 4-hour delay. They monitored fawns every 8 hours to ≥4 weeks of age and 1–3 times daily to 12 weeks of age. Observers estimated fawn locations via triangulation every 32 hours during their first 3 weeks of life (total 15 locations) according to the procedures described in Kilgo et al. (2014). Kilgo et al. (2012) and Kilgo et al. (2014) provide additional details on female and fawn capture, handling, and monitoring procedures. Researchers conducted deer capture and handling under the authority of a South Carolina Department of Natural Resources Research Collection permit (no. 120406-01) and followed taxon-specific guidelines for the use of wild vertebrates in research to ensure animals were treated ethically and humanely (Sikes et al. 2011).

Observers confirmed predation as the cause of death at carcass recovery sites when killing bite wounds (evidenced by subcutaneous trauma) were present on the head and neck (when available). They determined the species of predator responsible using a combination of field and genetic methods, as described in Kilgo et al. (2012). Briefly, field evidence included presence of tracks, patterns of consumption, and caching characteristics. Observers swabbed residual predator saliva from recovered carcasses or collars for genetic evidence. Although scavenging was a potential confound, field crews never observed evidence of predator presence with a lack of killing bite wounds. In addition, the frequent monitoring schedule was designed to minimize the likelihood of scavenging prior to investigator arrival. Thus, when predator evidence was present at mortality sites, cause of death was attributed to that predator. We were only interested in the role of landscape characteristics in coyote predation on fawns. Therefore, we censored the final dataset to include only those fawns killed by coyotes or surviving to 12 weeks, after which weekly survival rates were ≥0.95 (Kilgo et al. 2012).

Macrohabitat Characteristics

To determine whether landscape characteristics within fawn home ranges affected mortality risk, we first needed to estimate the area a fawn would use during the period of interest. However, we were not able to estimate individual fawn home ranges because most coyote-killed fawns (79%) died prior to 1 month of age, insufficient time to collect an adequate sample of point locations. Thus, we employed an approach similar to Rohm et al. (2007) and Grovenburg et al. (2012) by constructing fawn home ranges based on the average 95% minimum convex polygon home range area for a subset of fawns. Specifically, for a sample of 40 fawns with 15 telemetry locations each during their first 3 weeks of life, mean home range size was 29.1 ha (95% CI = 21.04–37.16 ha). Therefore, we created a 29.1-ha circular buffer around each fawn's capture location. We conducted this and all other geographic information system (GIS) operations using ArcMap 10.3.1 (Environmental Systems Research Institute, Redlands, CA, USA).

The lack of region-specific information on the effects of macrohabitat characteristics on fawn predation risk left some uncertainty in how to classify the landscape and, specifically, what constitutes edge. Gates and Gysel (1978) hypothesized that high-contrast edges, like those between fields and forests, might harbor greater prey densities, leading predators to view them as better foraging areas. Alternatively, predators might use edges to facilitate travel (Bider 1968), which would be especially important for coursing predators like coyotes. Thus, we implemented 2 landscape classification schemes, each designed to explore whether one of these 2 edge-related predation mechanisms was more relevant for fawns in the Southeast.

We obtained land cover and timber harvest data from 2015 SRS United States Forest Service timber stand maps. We used 2 schemes to classify forested stands, with each scheme designed to evaluate 1 of our 2 hypotheses related to the role of edge in coyote predation on fawns. In the first scheme, we included only high-contrast edges in the calculation of edge. Thus, we separated forest classes only according to recent harvest treatment (harvest only [HO]), which included unharvested, thinned, and clearcut. We obtained these data via timber sales records. Thinned included stands thinned ≤5 years prior, clearcut included 1–7-year-old regenerating stands, and unharvested included all stands not thinned or clearcut within those timeframes relative to each study year. In the second scheme, we included all edges possibly serving as travel corridors in the calculation of edge. On the SRS, most hardwood and pine stands are separated by firebreaks approximately 3 m wide. Because firebreaks potentially serve as coyote travel corridors, we also separated forest classes according to stand type (harvest and type [HT]) in the second classification scheme. This resulted in 6 forest classifications: pine unharvested, pine thinned, pine clearcut, hardwood unharvested, hardwood thinned, and hardwood clearcut. Other land cover classes included roads, utility rights-of-way, and fields. However, none of these classes represented >2% of the area contained within fawn home ranges and were not explicitly included in any of our models, other than in calculations of total edge. Maxie et al. (2010) cautioned against the use of unvalidated remotely sensed land cover maps in studying wildlife-habitat relationships. However, the classifications we used in each scheme were consistent with their recommendation to restrict analyses reliant on such data to broader classifications (e.g., pine forest vs. hardwood forest) to avoid spurious conclusions.

We expected recently thinned areas and regenerating clearcuts, regardless of stand type, to contain significant amounts of dense vegetation near ground level because of increased sunlight penetration following timber harvest. To evaluate this assumption, we used the visual obstruction data (0–4 index) from Kilgo et al. (2014) to calculate average visual obstruction ≤1 m from ground level, by cover class. Following classification of land cover for each scheme, we converted polygon shapefiles to rasters with 30 × 30-m

Table 1. Description of landscape- and class-level covariates used to model the effects of home range composition on coyote predation risk for white-tailed deer fawns on the Savannah River Site, South Carolina, USA, 2007–2012.

Variable name	Metric type	Definition (units)[a]
Total edge	Landscape	Length (m) of boundaries shared between different patch types
Shannon's diversity index	Landscape	Measure of relative patch diversity
Interspersion juxtaposition index	Landscape	Measure of patch adjacency
$\bar{x}$ patch fractal dimension	Landscape	Measure of shape complexity
$\bar{x}$ forest patch size	Class	Average patch size (ha) for all forest type patches
Thinned cover	Class	Total forested area (ha) thinned ≤5 yr prior
Clearcut cover	Class	Total area (ha) clearcut ≤7 yr prior
Thinned patch density	Class	Density (no./100 ha) of forested patches thinned ≤5 yr prior
Clearcut patch density	Class	Density (no./100 ha) of forested patches clearcut ≤7 yr prior
Pine forest cover	Class	Sum of areas (ha) of all pine forests not recently thinned or clearcut
Hardwood forest cover	Class	Sum of areas (ha) of all hardwood forests not recently thinned or clearcut
$\bar{x}$ pine patch size	Class	Average patch size (ha) for pine forests not recently thinned or clearcut
$\bar{x}$ hardwood patch size	Class	Average patch size (ha) for hardwood forests not recently thinned or clearcut

[a] See McGarigal et al. (2002) for additional information on covariates.

resolution. We used the Patch Analyst© extension (Rempel et al. 2012), which provides a user interface to FRAGSTATS (McGarigal et al. 2002) in ArcMap, to quantify landscape- and class-level variables of interest within fawn home ranges (Table 1). To calculate edge metrics, we defined edges (the area where 2 different land cover classes joined) as one pixel (30 × 30 m) in size. We calculated edge using 6 land cover classifications (3 forest types, roads, utility rights-of-way, fields) in HO modeling and 9 land cover classifications (6 forest types, roads, utility rights-of-way, fields) in HT modeling. McGarigal et al. (2002) provide additional information on calculation of edge and other metrics within FRAGSTATS.

Predation Risk

We used Cox proportional hazards regression models (Cox 1972) in the R software (R Core Team 2015) package survival (Therneau and Grambsch 2000, Therneau 2015) to estimate the effects of landscape and class covariates on hazard ratios. Hazard ratios typically provide estimates of the ratio of the hazard rate in treated versus control groups (Nakagawa and Cuthill 2007). In this case, we compared the ratio of hazard rates across the range of observed values for each habitat covariate for surviving versus coyote-depredated fawns to determine predation risk.

We constructed a set of candidate models for each of the 2 forest classification schemes. We used the best-supported model describing fawn survival from Kilgo et al. (2012), which included a within-year quadratic time trend and ordinal date of birth as the underlying model structure for all candidate models. The model set for HO consisted of 10 *a priori* Cox proportional hazards models, whereas the model set for HT consisted of 12 *a priori* models (Table 2). In addition to the hypotheses related to size, shape, and arrangement of patches within landscapes and the 2 edge hypotheses, we also used the differences in each classification scheme to examine the role of forest type (i.e., hardwood vs. pine) in coyote predation on fawns. We used Pearson's product-moment correlation coefficient to test for correlation among all pairs of predictors within models. We included only predictors with coefficients $|r| < 0.7$ in the same model. Annual coyote removal efforts during 2010–2012 affected coyote abundance and fawn survival on SRS, however, treatment effects varied among years (Kilgo et al. 2014). Thus, we also included year in the underlying model structure as a stratification variable to avoid any confounding effects of the removal treatment.

We used corrected Akaike's Information Criterion (AIC_c) and Akaike weights (w_i) to evaluate the strength of evidence among competing models included in HO and HT. We used the same procedure to compare the edge model from each candidate set. We included models within ≤4.0 AIC_c units of the best approximating model in our confidence set of models (Burnham and Anderson 2002). We considered predictors from our confidence set of models informative when 85% confidence intervals associated with their scaled parameter estimates did not overlap zero (Arnold 2010). We also used the survival package in R to test the proportional hazards assumption for all candidate models and found no evidence for statistically significant violations of proportionality in any of the predictor variables contained in those models (all $P > 0.05$). Although very few fawns were censored ($n = 3$), censoring resulted from an inability to monitor fawns, not from destruction of transmitters or another factor that would have increased or decreased mortality risk of censored fawns (Kilgo et al. 2012).

The objective of this analysis was to quantify the biological effects of each covariate on predation risk. Therefore, we converted coefficients for each informative parameter to hazard ratios. We interpreted these as statements of odds of coyote predation for a fawn given a certain value of a covariate. Because we used scaled covariates, we scaled hazard ratios according to the covariate-specific standard deviation. For example, a hazard ratio of 2, given a covariate with a standard deviation of 100 units (e.g., m), would mean a 2-fold change in predation risk for each 100-unit change in the covariate. We also used coxsimLinear in the R package simPH (Gandrud 2015) to simulate the effects of each informative predictor on hazard ratios, across their range of observed values. The simulation draws 1,000 values of the model coefficients from a multivariate normal distribution with means equal to the coefficient estimates and their respective variance and covariance (Gandrud 2015). We then used these quantities to

Table 2. Hazard ratio models, ranked according to Akaike's Information Criterion scores corrected for small sample size (AIC_c) and model weights (w_i), for white-tailed deer fawns on the Savannah River Site, South Carolina, USA, 2007–2012. In the harvest only scheme, forested patches were separated only according to timber harvest (i.e., unharvested, thinned, clearcut), whereas forested patches in the harvest and type scheme were separated according to timber harvest and stand composition (i.e., hardwood vs. pine).

Model[a]	K[b]	AIC_c	ΔAIC_c	w_i
Harvest only (HO)				
Edge	3	595.8	0.0	0.36
Patch size and shape	3	597.6	1.8	0.15
Diversity	3	597.6	1.8	0.14
Forest size	3	598.3	2.5	0.10
Null	2	598.7	2.9	0.08
Evenness	3	599.2	3.4	0.06
Edge and cover	5	599.6	3.8	0.05
Cover patch density	4	600.7	4.9	0.03
Cover	4	602.0	6.2	0.02
Global	10	609.6	13.8	0.00
Harvest and type (HT)				
Evenness	3	598.0	0.0	0.18
Edge	3	598.1	0.0	0.18
Diversity	3	598.6	0.6	0.14
Null	2	598.7	0.7	0.13
Forest size	4	599.9	1.8	0.07
Hardwood forest	3	600.0	2.0	0.07
Pine forest	3	600.0	2.1	0.07
Patch size and shape	3	600.5	2.5	0.05
Cover patch density	4	600.9	2.9	0.04
Edge and cover	5	601.7	3.7	0.03
Cover	4	601.7	3.7	0.03
Global	14	612.4	14.4	0.00
Comparison of edge				
HO edge	3	595.8	0.0	0.64
HT edge	3	598.1	2.3	0.21
Null	2	598.7	2.9	0.15

[a] Null models included only the base structure, whereas global models included all covariates from the candidate model set. Edge = total edge, patch size and shape = $\bar{x}$ patch fractal dimension, diversity = Shannon's diversity index, forest size (HO) = $\bar{x}$ forest patch size, evenness = interspersion juxtaposition index, edge and cover = total edge + thinned cover + clearcut cover, cover patch density = thinned patch density + clearcut patch density, cover = thinned cover + clearcut cover, forest size (HT) = $\bar{x}$ pine patch size + $\bar{x}$ hardwood patch size, hardwood forest = hardwood forest cover, pine forest = pine forest cover.

[b] Number of parameters estimated. All models had the base structure of the top model from the survival analysis from Kilgo et al. (2012), which included a within-year quadratic time trend and ordinal date of birth, plus year as a stratification variable.

calculate hazard ratios with posterior distribution quantiles. We plotted results using the simGG command in the simPH package.

RESULTS

The dataset consisted of 216 fawns, 192 of which were captured from 163 monitored VITs. Censoring to include only those fawns killed by coyotes or surviving to 12 weeks reduced the sample to 175 fawns. We removed an additional 10 fawns from the dataset because of missing or inadequate stand composition data within their simulated home ranges, bringing the final sample of fawns for the current study to 165.

As predicted, average visual obstruction ≤ 1 m in height was greater in clearcut ($\bar{x} = 2.58 \pm 0.10$ [SE]) and thinned ($\bar{x} = 2.27 \pm 0.10$) areas, than in unharvested ($\bar{x} = 1.94 \pm 0.02$) areas. However, our prediction that hazard ratios would decrease as the area or density of these patches in fawn home ranges increased was not supported (Tables 2 and 3). The average amount of edge in fawn home ranges was greater for the HT ($\bar{x} = 2{,}097 \pm 1{,}115$ [SD] m, range = 0–4,800 m) than the HO ($\bar{x} = 990 \pm 968$ m, range = 0–3,960 m) classification scheme, and our prediction that hazard ratios would decrease as edge within fawn home ranges increased was supported. Under the HO scheme, the edge model received an Akaike weight of 0.36, making it more than twice as likely as the next most supported model, which included terms for patch size and shape. For each 1-standard deviation (SD)-unit (968 m) decrease in edge within a fawn's home range, probability of coyote predation increased 1.26 times (Table 3 and Fig. 1). Further, a fawn with the least amount of edge in its home range was >2 times more likely to be depredated by a coyote than a fawn with the greatest amount of edge in its home range (Fig. 1). The edge model was also highly ranked in the HT scheme; however, there was little support for any particular model in the HT candidate set. Specifically, all models (except the global) were within ≤ 4.0 AIC_c units of the best approximating model. In the comparison of edge models from each scheme, the model from HO received an Akaike weight of 0.64, making it >3 times as likely as the edge model from the HT scheme (Table 2).

Table 3. Scaled parameter estimates, standard errors, and 85% confidence intervals for informative predictor variables included in the confidence set of models describing the effects of landscape and class characteristics on hazard ratios for white-tailed deer fawns on the Savannah River Site, South Carolina, USA, 2007–2012. In the harvest only scheme, forested patches were separated only according to timber harvest (i.e., unharvested, thinned, clearcut), whereas forested patches in the harvest and type scheme were separated according to timber harvest and stand composition (i.e., hardwood vs. pine).

Variable	β	SE	85% CI	Odds ratio	85% CI	Scalar (units)
Harvest only (HO)						
Total edge	−0.23	0.11	−0.39 to −0.07	1.26	1.07–1.48	968 (m)
$\bar{x}$ patch fractal dimension	−0.19	0.11	−0.35 to −0.03	1.21	1.03–1.42	0.04
Shannon's diversity index	−0.18	0.11	−0.34 to −0.02	1.20	1.02–1.40	0.36
$\bar{x}$ forest patch size	0.16	0.11	0.00 to 0.32	1.17	1.00–1.38	9.31 (ha)
Harvest and type (HT)						
Interspersion juxtaposition index	−0.17	0.10	−0.31 to −0.03	1.19	0.97–1.03	34.29
Total edge	−0.17	0.10	−0.31 to −0.03	1.19	0.97–1.03	1,115 (m)
Shannon's diversity index	−0.15	0.10	−0.30 to −0.01	1.16	1.01–1.35	0.39
$\bar{x}$ hardwood patch size	0.24	0.13	0.05 to 0.43	1.27	1.05–1.54	8.45 (ha)

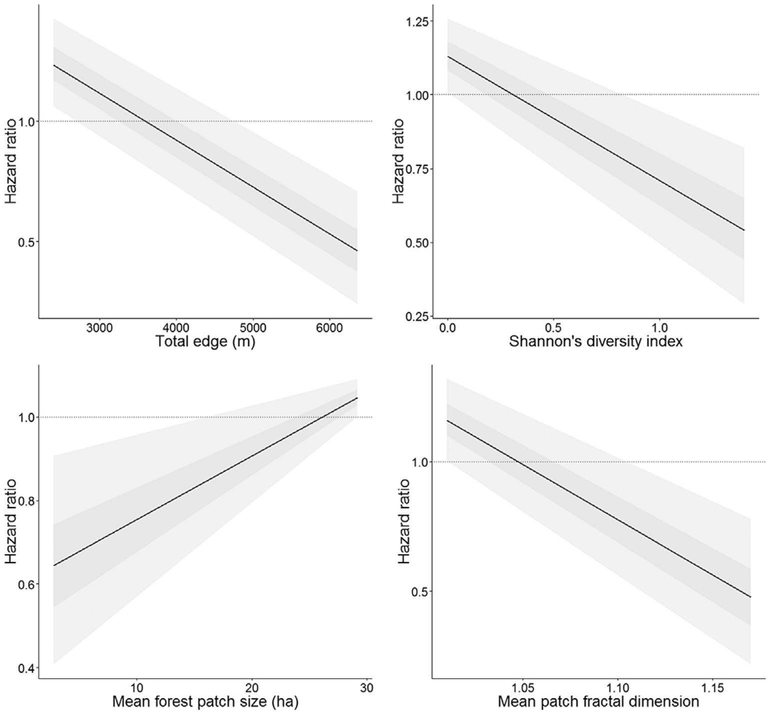

Figure 1. Simulation of the effects of informative landscape- and class-level predictors from the harvest only (HO) model set on hazard ratios for white-tailed deer fawns on the Savannah River Site, South Carolina, USA, 2007–2012. The extent of predictions was limited to the range of observed values for each predictor. Dotted line at $y = 1$ serves as a reference value at which hazards are equal. Light gray ribbons represent the lower (0.075) and upper (93.5) quantiles of simulated hazard ratios, whereas darker gray ribbons indicate the central 50% (0.25–0.75) of these values.

Other informative covariates from the HO scheme included mean patch fractal dimension, Shannon's diversity index, and mean forest patch size (Table 3). For each 1-SD-unit (0.04) decrease in mean patch fractal dimension (an index of shape complexity), the probability of coyote predation increased 1.21 times. For each 1-SD-unit (0.36) decrease in Shannon's diversity index, the probability of coyote predation increased 1.20 times. Mean forest patch size had the opposite effect on hazard ratios. For each 1-SD-unit (9.31 ha) increase in mean forest patch size, probability of coyote predation increased 1.17 times (Table 3 and Fig. 1). Despite the fact that there was little support for any of the HT models, the candidate set included 3 informative covariates other than edge: the interspersion and juxtaposition index, Shannon's diversity index, and mean hardwood patch size (Table 3 and Fig. 2). In general, probability of coyote predation tended to increase as landscape composition within home ranges became more homogeneous and contained less edge. Further, as mean patch size of hardwood forests increased, probability of coyote predation likewise increased.

DISCUSSION

Regardless of classification scheme, fawns with more edge in their simulated home ranges were less likely to be depredated by coyotes. This finding was consistent with our hypothesis based on work in Illinois (Rohm et al. 2007) and demonstrated that high-contrast edges were more relevant for coyote predation on fawns on SRS. However, these findings seem to contradict the mechanism proposed by Gates and Gysel (1978), wherein high-contrast edges might harbor greater prey densities, leading predators to view them as better foraging patches. It then follows that if coyotes perceived the higher contrast edges represented in the HO scheme as better foraging areas, predation risk for fawns should be greater, not lower, in fawn home ranges containing more edge. A change in coyote foraging preferences along edges could compensate for this effect. During May–June, when the majority of fawns were killed by coyotes, wild plums (*Prunus* spp.) and blackberries (*Rubus* spp.), species commonly associated with edges and open areas, were the most commonly occurring non-deer food items in coyote diets on SRS (Schrecengost et al. 2008). Although these food items may have increased the attractiveness of edges to coyotes, their relative abundance along edges potentially made them a more profitable prey choice. In fact, several have suggested high availability of non-deer food items could buffer fawn predation (Andelt et al. 1987, Burroughs et al. 2006).

Nonetheless, coyote foraging decisions and predation on fawns likely involve complex interactions among multiple landscape-scale characteristics. For example, Andrén (1995) proposed that the relationship between edge and predation rate is dependent on the configuration of habitat in the landscape. On SRS, fawns with home ranges containing more edge and a diversity of small, complex-shaped, well-interspersed patches were less likely to be depredated by coyotes. Predators select a foraging patch based on its productivity relative to that of surrounding patches (Brown and Litvaitis 1995). The relatively high configurational and

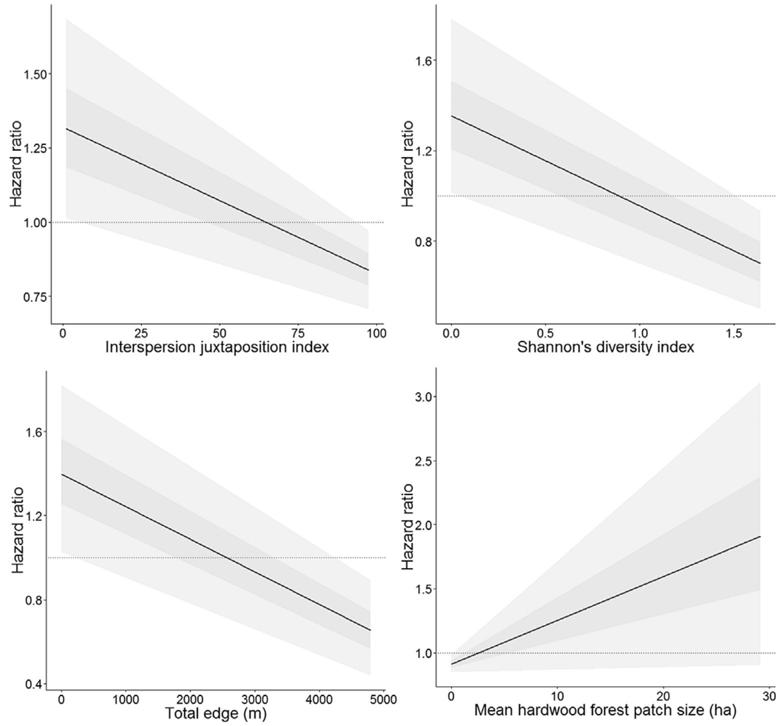

Figure 2. Simulation of the effects of informative landscape- and class-level predictors from the harvest and type (HT) model set on hazard ratios for white-tailed deer fawns on the Savannah River Site, South Carolina, USA, 2007–2012. The extent of predictions was limited to the range of observed values for each predictor. Dotted line at $y = 1$ serves as a reference value at which hazards are equal. Light gray ribbons represent the lower (0.075) and upper (93.5) quantiles of simulated hazard ratios, whereas darker gray ribbons indicate the central 50% (0.25–0.75) of these values.

compositional heterogeneity of some fawn home ranges on SRS may have diminished the ability of coyotes to identify productive patches (i.e., those containing $\geq$1 fawn). Others have suggested that patches with more convoluted edges might be more difficult for coyotes to search (Rohm et al. 2007), which might explain why predation risk decreased as mean patch fractal dimension increased on SRS. However, we consider these working hypotheses.

Rohm et al. (2007) also speculated that edges may provide higher quality habitat for females, allowing for maintenance of smaller home ranges and thereby additional time for nursing and defense of fawns from predators. However, an earlier analysis of the current dataset (Kilgo et al. 2012) did not support this hypothesis because fawn mass was not an important predictor of survival. Further, there is little evidence (Garner and Morrison 1980, Smith 1987) to suggest whitetail females attempt, or are successful in, defense of fawns from coyotes (Lingle et al. 2005).

Consistent with our prediction, we found that predation risk increased with increasing mean forest patch size, where visual obstruction was lower. Though an intuitive finding at first glance, coyote foraging efficiency is diminished in forested landscapes elsewhere in the United States (Gese et al. 1996, Richer et al. 2002), and large forest patches were conducive to fawn survival in Illinois (Rohm et al. 2007). None have examined coyote foraging efficiency in the Southeast, but coyotes in the Southeast generally prefer open habitats comprised of dense, early successional, vegetation over more forested ones (Holzman et al. 1992, Chamberlain et al. 2000, Schrecengost, et al. 2008, Hickman et al. 2015, Hinton et al. 2015). Thus, conflicting hypotheses remain regarding the role of each of these 2 cover types in coyote predation on fawns. Fawn predation risk might be greater in mature forests because of the relative lack of visual obstruction near ground level, or it might be lower because of coyote avoidance of these areas. On the other hand, fawn predation risk might be lower in open habitats because of increased visual obstruction near ground level, or it might be greater because of coyote preference for these areas. Our findings relative to the effects of mature forest on hazard ratios appear to support the visual obstruction hypothesis (i.e., predation risk was greater in mature forest). In contrast, we found no evidence to suggest that predation risk decreased in recently thinned and clearcut areas, which had greater visual obstruction.

The latter finding, at least, is consistent with work in North Carolina and a previous analysis of the current dataset (Kilgo et al. 2014, Chitwood et al. 2015*b*). Despite the fact that we examined the role of visual obstruction differently by quantifying the size, shape, and arrangement of high-visual-obstruction cover types in fawn home ranges, we found little evidence to support a role of these factors in coyote predation on fawns. Thus, it appears that visual obstruction, or indices thereof, may be of little significance in this predator-prey dynamic in the Southeast. However, recently thinned and clearcut areas combined represented only 12% of the total area within fawn home ranges on SRS, which potentially reduced our ability to detect a relationship between these predictors and hazard ratios. Perhaps more importantly, dense cover patches may become ecological traps when severely limited across the landscape (Chitwood 2014) though, unlike Kilgo et al. (2014), we found no evidence to suggest a negative effect of dense cover on predation risk either.

A potential drawback of our approach was its dependence on the assumption that circular buffers centered on fawn capture locations were representative of actual fawn home ranges. These buffers were sized based on site- and age-specific fawn home range data and it is unlikely that simulated home ranges were consistently biased towards, for example, areas containing more edge for surviving fawns and less edge for coyote-depredated fawns. Furthermore, the primary objective of this analysis was to determine how the shape, size, and arrangement of patches in the general vicinity of fawns influence predation risk, not the effects of conditions at a specific location on predation risk.

Clearly, there remains substantial uncertainty regarding how cover type and arrangement affect coyote predation on fawns in the Southeast. More research is needed in this area, especially in Southeastern landscapes with different forest management practices and landscape composition than SRS. Specifically, the relatively long forestry rotation lengths and large scale of consistent management on the SRS is atypical compared to most areas in the region. However, it would be logistically difficult and cost prohibitive to implement a manipulative experiment to further understanding of the role of landscape factors in fawn predation risk on a regional scale. This issue might be addressed through a cooperative research framework, with the methods implemented in this study applied to a variety of representative landscapes throughout the region.

Nevertheless, our findings underscore the importance of covariate and scale selection in studies examining the role of vegetation structure and composition in coyote predation on fawns. We encourage researchers to consider a wider variety of metrics when developing candidate model sets, instead of strictly those that may affect visual obstruction, because multiple landscape mosaic descriptors influence predator densities and foraging efficiency on the SRS and in other systems.

MANAGEMENT IMPLICATIONS

Coyotes will remain a significant predator of white-tailed deer fawns in the Southeast for the foreseeable future, and existing strategies to mitigate their impacts are sometimes impractical or inadequate. Therefore, we suggest managers also consider using forest management to increase the interspersion and diversity of stand types and ages in areas of concern. As indicated by our results, this practice may decrease predation risk of fawns and potentially increase recruitment. Furthermore, landscapes comprised of a diversity of stand types and ages are considered preferred habitat for white-tailed deer, a generalist species (Diefenbach and Shea 2011). Such landscapes also contain abundant edge. Thus, management for these conditions would potentially benefit deer populations in 2 ways: by decreasing fawn predation and increasing reproductive rates by enhancing overall habitat quality for deer. In contrast, we would expect coyote predation rates on fawns to be greater, and reproductive rates lower, in areas primarily comprised of mature, closed-canopy forests. However, we are the first to document an effect of landscape and class characteristics on coyote predation on fawns in the Southeast and suggest our findings be interpreted or extrapolated to other areas with caution.

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