Edge density affects demography of an exploited grassland bird

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Abstract. Humans modify landscapes for a variety of reasons including agriculture, urbanization, and to facilitate recreation. Landscape modifications can lead to complete loss of existing cover types and/or fragmentation of remaining cover types. Grasslands are one of the ecosystems most heavily impacted by human modifications; however, for many species, an understanding of how fragmentation affects population parameters is lacking. We investigated the influence of landscape fragmentation on survival, reproduction, and density using the northern bobwhite (Colinus virginianus), a facultative grassland species, as our case study. We experimentally manipulated the level of edge density (none, low, and high) of bobwhite management units and estimated seasonal survival, productivity, and autumn densities. Winter survival was lower in edge density treatments, relative to the control. An increase in migratory raptor density during the winter, along with a decrease in thermal refugia, may be contributing to lower winter survival in edge density treatments. Fecundity was higher in the edge density treatments, relative to the control, and was negatively related to winter survival. Similarly, breeding season survival was higher in more fragmented sites. This indicated a density-dependent relationship, where lower bird densities at the beginning of the breeding season possibly led to greater resource availability, and thus survival and productivity, of the birds that remained. However, a density-dependent response in breeding season survival and productivity was not enough to offset the negative impact of edges in the low edge density sites. Consequently, autumn density was lower relative to both control and high edge density treatments. Our study demonstrates the importance of capturing the entire life cycle when exploring the relationship between landscape pattern and population parameters.

Key words: density; edge density; fragmentation; known-fate; Northern Bobwhite; productivity; spatial capture–recapture; survival.

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INTRODUCTION

Landscapes are modified to provide ecosystem services for humans such as provisioning, regulating, and cultural services (e.g., recreational benefits; Mitchell et al. 2015, Lamy et al. 2016). In systems where harvest occurs, landscapes are modified to facilitate the abundance of game animals, increase the encounter rate with game animals, and improve conditions for the hunters themselves. Modifications to facilitate recreation often result in the development of internal edges (e.g., hiking trails, hunting paths; Miller et al. 1998). These modifications can alter the amount of existing cover types (Leung and Marion 2000) and can lead to increased
landscape fragmentation, in turn increasing the amount of edge and altering interspecies interactions (Wilson et al. 2010).

Increasing edge has been shown to impact wildlife behavior and demography. Population size for some bird species has been shown to decrease with increasing proximity to edges (bobolinks, Fletcher and Koford 2003; chesnut-collared longspurs and Sprague’s pipits, Sliwinski and Koper 2012). Some bird species flush in response to human activity near edges (Thiel et al. 2007) or avoid using breeding or nesting habitat within their home ranges near edges (Winter et al. 2000, Coppes et al. 2017). Other species nest near edges but experience higher rates of nest predation or brood parasitism in smaller habitat fragments (Robinson et al. 1995) and closer to edges (Miller et al. 1998, Winter and Faaborg 1999, Winter et al. 2000; see Benson et al. [2013] for a review of empirical evidence). Regardless of the mechanism, landscape modifications for outdoor recreation could lead to a decline in population density and changes in species composition (Van der Zande et al. 1984, Miller et al. 1998, Ribic and Sample 2001, Perkins et al. 2003). However, the influence of internal edges in the context of modifying landscapes for recreation is understudied, particularly its influence on vital rates (e.g., fecundity and survival) that drive variation in avian population density.

Grasslands are one of the ecosystems most heavily impacted by human activity (Steinauer and Collins 1996). In addition to direct loss of this cover type, remaining patches of grassland are often more fragmented and isolated (Steinauer and Collins 1996). Research has linked the decline in amount and increase in isolation of remaining fragments to the decline of many obligate and facultative grassland species (Herkert et al. 2003). Several recent reports show that grassland birds are among taxa experiencing the greatest population declines in North America since the 1970s (Wilsey et al. 2019). The northern bobwhite (Colinus virginianus) is a ground-nesting, facultative grassland species that has experienced precipitous population declines throughout its historical range (Brennan 1991, Link et al. 2008). Loss of grasslands has been implicated as a major driver of these declines (Burger 2002). In areas where bobwhites are still harvested, managers often mow hunting paths into habitat patches to increase hunter accessibility and provide travel lanes for pointing dogs (e.g., McGrath et al. 2018). Mowing reduces the amount of cover, but also increases internal edge density. Higher edge density, at least for woody edges, has been negatively correlated with male bobwhite call counts (Guthery et al. 2001). However, to our knowledge there are no experimental studies that have investigated the impact of variation in edge density, internal or otherwise, on the full annual life cycle of any grassland bird species. Quantifying the relationship between edge density and population parameters is important not only for grassland bird conservation and management, but also for testing predictions from ecological theory. Specifically, how do populations respond to an increased density of habitat edge created by unnatural fragmentation?

We explored the influence of landscape modifications for outdoor recreation (i.e., hunting) on population density, survival, and reproduction, using a population of northern bobwhite in north Florida as a case study. Specifically, we experimentally manipulated edge density by applying three mowing treatments to landscapes in autumn for three years: a control (i.e., no mowing), a low edge density treatment, and a high edge density treatment. The mowed lanes were intended to improve walking conditions for hunters and increase encounter rates between hunting dogs and bobwhite coveys, but the possible consequences they have on population parameters is unknown. We tested the prediction that survival would be lower in landscapes with higher edge density (Fig. 1A, B). Higher edge density could make it easier for raptor species to locate bobwhite prey (i.e., visually within the mowed lanes), relative to landscapes with lower edge density (Perkins et al. 2014, Atuo and O’Connell 2017). In addition, landscapes with higher edge density have less tall vegetation that could provide thermal refugia during the winter (Wiseman and Lewis 1981). We tested the prediction that productivity would also be lower in landscapes with higher edge density (Fig. 1A). Like other grassland bird species, bobwhite may experience higher rates of nest predation near edges and consequently lower productivity (e.g., Winter et al. 2000). Given a decrease in survival and reproduction, we predicted lower autumn
population density, in higher edge density treatments (Fig. 1A). However, density-dependent processes may mediate the negative impacts of higher edge density treatments (Fig. 1B; McConnell et al. 2018). Lower winter survival may be offset by an increase in reproductive output (mediated by lower spring population densities) in the higher edge density treatments (Fig. 1B). Consequently, there would be no difference in autumn population density among treatments (Fig. 1B). Our study contributes to understanding how landscape modification for recreation affects population dynamics and highlights the importance of considering a populations’ full annual life cycle.

**METHODS**

**Study site**

Research was conducted on the 1616 ha property owned by Tall Timbers (a non-profit organization), located in northern Leon County, Florida, USA (Fig. 2). The climate of the study area is driven by its proximity to the Gulf of Mexico with relatively mild winters and hot humid summers with average annual temperature of 20°C, average monthly maximum temperatures during summer of 33–36°C, and average minimum temperatures during winter of 2–9°C. The area receives an average of 137 cm of precipitation each year. The study area is managed for bobwhite and to mimic the historical pine savannah ecosystem. The overstory consists mostly of loblolly (Pinus taeda) and shortleaf pine (P. elliottii) throughout the uplands, and the lowlands consist mostly of hardwoods (e.g., Quercus spp.). The understory is mostly old-field vegetation consisting of native grasses (e.g., Andropogon spp.), shrubs (e.g., Rubus spp.), and legumes (e.g., Desmodium spp.). Prescribed fire is applied every other year in a mosaic pattern across the entire area resulting in about 50% of the area burned each spring. The average fire return interval is two years.

**Experimental manipulation of landscape structure**

The study area was divided into three management units (approximately 230 ha each, Fig. 2). Treatments were randomly assigned to each
management unit \((n = 3)\) during year one of the experiment (2014). Treatments were than rotated clockwise, each subsequent year (2015, 2016) to ensure that each management unit received each treatment (Fig. 2). Thus, each treatment was replicated three times across the three years, but spatial replication and temporal replication are confounded. We considered three treatment levels that increased in edge density and decreased in habitat amount: control (control; no mowing), low edge density (low; \(27.43 \times 27.43\) m spaced mowed grids), and high edge density (high; \(9.14 \times 9.14\) m spaced mowed grids; Figs. 2, 3). Within each management unit, between four and five 25 ha quadrats were established for conducting covey call surveys (see Monitoring bobwhite populations for details). Quadrats within the control treatment had no linear edge, quadrats within the low treatment had an average of \(9164\) m linear edge per quadrat, and quadrats in the high treatment had an average of \(15,067\) m linear edge per quadrat. Relative to the control, low quadrats had an average of 20% cover removed and high

Fig. 2. Tall Timbers study area located in Leon County, Florida, USA. Bold polygons represent the outline of each management unit that was assigned to one of three mowing treatments (control, low, and high). White square polygons represent quadrats used to conduct covey call surveys. Landcover was the same across all three years of the study (2014–2016).
quadrats had an average of 35% cover removed. The mowed strips were <10 cm in height, whereas un-mowed areas averaged 30 cm. Mowing occurred only once each year during late October–early November, according to assigned treatment level for that year. Hence, by the start of the breeding season (April 15th), variation in edge density and cover amount had begun to dissipate among treatments.

Monitoring bobwhite populations

Bobwhite (from a wild population) were captured during October and January each year using walk-in funnel traps baited with grain sorghum. Between four and six individuals per covey (social group of bobwhites) were radio-tagged with 6.2-g necklace-style transmitters, for a total of approximately 50 individuals per management unit (250 ha) each year. Radio-tagged individuals were located at least two times per week during the non-breeding season and a minimum of three times per week throughout the breeding season, and the fate (dead, alive) was recorded. If the number of individuals alive dropped below 50 during the study, new individuals were tagged. We located radio-tagged individuals with a mortality signal and classified cause of predation based on the condition of the radio-collar (e.g., tracks nearby, bite marks, bent antenna), condition of the bird (e.g., scattered remains vs. feather pile), or location of the transmitter (e.g., in a tree, burrow, ground). Harvested birds were recovered and reported directly by hunters. During the breeding season, nests were located and checked daily (using telemetry from afar) and the fate of the nest was followed until eggs hatched or were destroyed (e.g., predation and weather). The number of eggs per nest was recorded, and the fate of each egg (hatched, destroyed) was also recorded.

We used covey call count surveys (Wellendorf et al. 2004) conducted during mid-October to late November using the quadrat-sampling method to estimate autumn bobwhite density. The timing of the fall surveys that occur after the fall in which the treatment is applied is a product of all population processes (e.g., survival, reproduction, and recruitment to the population surveyed in the fall) that occur during the year and in response to the treatment. The quadrat method employs a 25 ha (500 × 500 m) quadrat and

Fig. 3. GPS tracks of dogs (red and blue) and hunters (yellow) during quail hunts in management units with three different edge density treatments (control, low, and high) on Tall Timbers, Leon County, Florida, USA.
multiple observers to survey calling coveys. A total of four observers were required, with one observer positioned along the midpoint of each quadrat side (north, east, south, west). Observers listened for the koi-lee covey calls (Stoddard 1931) given by bobwhites, almost always 20–25 min before sunrise, and recorded the locations of calling coveys on aerial photographs. Bird dogs were used to systematically search the sampling area to validate coveys heard and obtain individual covey sizes via pointing and flushing. At the conclusion of each survey, observers compared their results to determine whether a detected covey was inside or outside of the quadrat. Observers also assembled a summary data sheet that included the location of each covey and which of the four observers heard that covey calling. In this way, we obtained a spatially explicit detection history for each covey, for each quadrat, in each year.

**Productivity**

We modeled the number of nests initiated (nest propensity), clutch size, and number of female chicks produced per hen (fecundity) as a function of our edge density treatments. We modeled the number of nests initiated per individual (including males) using a Poisson model. Male northern bobwhite are known to incubate nests (DeVos and Mueller 1993), and so we included their potential contribution to the number of nests within each treatment.

\[
\text{nests}_i \sim \text{Poisson}(\lambda_{ni}),
\]

\[
\lambda_{ni} = \exp(C_n + L_n \text{low}_i + H_n \text{high}_i),
\]

where \(C_n\) represents the coefficient for the reference level (control, un-mowed treatment), \(L_n\) represents the difference between the low edge density treatment and the control, and \(H_n\) represents the difference between the high edge density treatment and the control. The dummy indicator variables \(\text{low}_i\) (low edge density treatment) and \(\text{high}_i\) (high edge density treatment) are coded as 0 or 1 and indicate whether each individual \(i\) was found within either of the two treatments. Here, nests, was data and represents the number of nests initiated per individual during our study. We modeled nests initiated as a random variable from a Poisson distribution because bobwhite are known to initiate multiple nests during the breeding season (DeVos and Mueller 1993).

We also modeled clutch size using a Poisson model:

\[
\text{clutchsize}_{i,n} \sim \text{Poisson}(\lambda_{ci} \times \text{nests}_{i,n}),
\]

\[
\lambda_{ci} = \exp(C_c + L_c \text{low}_i + H_c \text{high}_i),
\]

where \(C_c\) represents the coefficient for the reference level (control, un-mowed treatment), \(L_c\) represents the difference between the low edge density treatment and the control, and \(H_c\) represents the difference between the high edge density treatment and the control. The dummy indicator variables \(\text{low}_i\) (low edge density treatment) and \(\text{high}_i\) (high edge density treatment) are coded as 0 or 1 and indicate whether each individual \(i\) was found within either of the two treatments. Here, we can think of \(\lambda_{ci}\) as a metric for functional nest success (i.e., the proportion of eggs within a clutch that are expected to hatch). The number of chicks produced by each individual \(i\), in each clutch \(n\), \(\text{chicks}_{i,n}\) that hatched from each nest was not always recorded, so in these cases the number of chicks was treated as an unknown quantity to be estimated from the model. We converted the number of chicks produced per nest, per individual to the number of females produced per hen (i.e., fecundity).
Survival

We assumed that the fate of each individual was known, during each capture period, and used a known-fate model to estimate weekly survival rates for radio-tagged birds (White and Garrott 1990):

\[ y_{i,t} \sim \text{Bernoulli}(y_{i,t-1} \times \phi_{i,t}), \]

where \( y_{i,t} = 1 \) indicates bird \( i \) was alive during week \( t \) and \( y_{i,t} = 0 \) indicates bird \( i \) was found dead during week \( t \). \( \phi_{i,t} \) represents the survival probability for individual \( i \) in week \( t \). We used a logit-linear model to estimate the effect of edge density and season on survival \( \phi_i \), where the survival probability for bird \( i \) in week \( t \) is estimated as:

\[ \text{logit}(\phi_{i,t}) = \beta_jX_i. \]

Similar to our model for productivity, \( \beta_j \) is the vector of treatment-specific fixed effects and \( X \) is a matrix indicating the edge density treatment (i.e., control, low, high) and season (i.e., non-breeding, breeding) for each bird. We included the main effect of treatment and season, as well as the interaction between treatment and season.

Autumn density

We estimated autumn densities using covey call surveys and a spatial capture–recapture model (Borchers and Efford 2008, Royle et al. 2013). Our data \( y_{i,g,j} \) was arranged as a 3-D array with dimensions equal to the number of individuals, the number of quadrats, and the number of observers per landscape. If \( y_{i,g,j} = 1 \), that represents a detection of individual \( i \) by observer \( j \) in quadrant \( g \). If an individual was not detected by a given observer in a quadrant, \( y_{i,g,j} = 0 \). We excluded those individuals that were located outside of each quadrant. Because we do not know the number of individuals in each unit, we set an upper limit \( M \) of the total number of possible coveys and augment our observed data, \( n \) (i.e., counts of calling coveys), with \( M-n \) potential coveys (i.e., \( y_{i,g,j} = 0 \) for all observers). Whether an individual covey was estimated to occur within a landscape, then becomes \( z_{i,g} \sim \text{Bernoulli}(\lambda_g/M_g) \), where \( \lambda_g \) is the expected covey density and \( M_g \) represents the number of coveys detected plus the augmented detection histories, per landscape. We sum the coveys \( z_i \) as the interaction between treatment and season.

\[ g = 1 \] estimated to occur within each quadrant and divide by quadrant area to obtain covey density within each treatment. We converted covey density to the density of individuals by multiplying our quadrat specific densities by the average covey size (\( n = 13.5 \)) in our study system.

We modeled expected covey density within each quadrant \( g \) as a log-linear function of our treatments (control, low, high):

\[ \lambda_g = \exp\left(\beta_{1\text{control}}g + \beta_{2\text{low}}g + \beta_{3\text{high}}g\right), \]

where \( \beta_1, \beta_2, \) and \( \beta_3 \) represent the coefficients for the control, low, and high edge density treatments. Treatment was represented by three dummy variables coded as 0 or 1 such that the model had three intercepts.

The activity center of a covey within each quadrant is assumed to be distributed uniformly within a quadrant \( S_g \):

\[ s_{i,g} \sim \text{Uniform}(S_g). \]

The detection probability \( p \) for each individual was modeled as a function of the distance between an individual’s activity center \( s_{i,g} \) and each observer:

\[ p_{i,g,j} = \exp\left(-\frac{d_{i,g,j}^2}{2\sigma^2}\right), \]

where \( \sigma \) represents the scale parameter of the half normal detection function and \( d_{i,g,j} \) is the distance between individual \( i \)'s activity center and observer \( j \) within quadrant \( g \). The model for the data \( y_{i,g,j} \) then becomes:

\[ y_{i,g,j} \sim \text{Bernoulli}(p_{i,g,j} \times z_{i,g}), \]

whereby the detection–non-detection data, \( y \), depend on whether the covey is located within the quadrant, \( z \), and the detection probability, \( p \).

Model fitting

We fit all models in a Bayesian framework using rjags (Plummer 2016) called from R (R Development Core Team 2013). We assessed model convergence using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) and by visually inspecting the chains for mixing. We retained 10,000 iterations per Markov chain (\( n\text{chains} = 3 \)), after discarding 100 iterations for adaptation.
To evaluate model fit, we conducted posterior predictive checks (Gelman et al. 2000). For our productivity analysis, we compared observed data on the mean number of chicks produced per individual to data simulated from posterior distributions of parameters estimated in our model during each MCMC iteration. We plotted the posterior distribution of mean chick production from our model and compared that distribution to the mean number of chicks observed in our empirical data. In a similar manner, we compared the posterior distribution of mean number of weeks individuals survived to the mean observed in our data. For our model of autumn density, we evaluated the observation component of the model, using a fit statistic based on a summary of the observed data (Gelman and Hill 2006, Royle et al. 2013). For each MCMC iteration, we computed a replicate data set $y_{rep,ij}$ and calculated quadrat encounter frequencies. We calculated a fit statistic from the Freeman-Tukey residuals from our actual and replicate data sets that are conditional on the collection of all parameters in our model. Finally, we calculated the Bayesian $p$ value for the fit statistic; a value close to 0 or 1 may indicate poor model fit (Gelman and Hill 2006). As a more holistic measure of model fit, we calculated the expected number of individuals detected for each MCMC iteration, given the state and detection model and constructed a 95% credible interval. We compared this interval to the observed number of individuals detected in our data (Proffitt et al. 2015). Observed quantities that fell outside of this interval would indicate poor model fit.

We report posterior means, credible intervals, and posterior probabilities of the difference in the effect of edge density treatment on bobwhite vital rates. Posterior probabilities (posterior $p$ values) are the probability an effect was greater than zero, given a model of bobwhite vital rates. We considered an effect significant when the posterior $p$ value was >0.95. All R code for fitting our models and evaluating model fit is provided with data in our Figshare repository (https://doi.org/10.6084/m9.figshare.12009228.v1).

**RESULTS**

Over the course of our study, we radio-tagged and tracked 872 unique individuals. We located 308 nests (2014, $n = 94$; 2015, $n = 110$; 2016, $n = 104$) and documented an average clutch size of 12.77 (2014, $n = 12.12$; 2015, $n = 12.80$; 2016, $n = 13.24$). Of the nests initiated, 57% successfully hatched (2014, $n = 0.57$; 2015, $n = 0.62$; 2016, $n = 0.53$), with an average number of 5.87 chicks produced per nest (2014, $n = 4.06$; 2015, $n = 6.21$; 2016, $n = 7.14$). Across all three years, of the nests that successfully hatched (i.e., at least one egg hatched), 85% of eggs (2014, $n = 0.87$; 2015, $n = 0.84$; 2016, $n = 0.86$) hatched for an average of 11.02 chicks produced per clutch (2014, $n = 10.05$; 2015, $n = 11.38$; 2016, $n = 11.26$). The number of unique coveys heard calling varied over time (2014, $n = 67$; 2015, $n = 82$; 2016, $n = 79$), and the average covey size varied by year (2014, $n = 13$; 2015, $n = 13.50$; 2016, $n = 14$).

For our models of productivity, survival, and autumn density, the Gelman-Rubin diagnostic for all coefficients (all values between 1.0 and 1.10) and inspection of trace plots indicated convergence and appropriate mixing of the Markov Chains (Appendix S1: Figs. S1, S2, S3). The observed mean number of chicks produced was within the posterior distribution of chicks produced estimated by our productivity model (Appendix S1: Fig. S4). For our survival analysis, the observed mean number of weeks survived was within the posterior distribution of mean number of weeks survived estimated from our known-fate model (Appendix S1: Fig. S5). For our density model, the Bayesian $p$ value for the detection process each year did not indicate a lack of model fit (2014, $P = 0.64$, 2015, $P = 0.23$, 2016, $P = 0.32$). The observed number of individuals each year was within the 95% credible intervals for the expected number of individuals each year, again indicating no lack of model fit (Appendix S1: Fig. S6).

Fecundity (i.e., number of female chicks produced per female) was lower in the control relative to both low and high edge density treatments (Fig. 4A, Table 1). Functional nest success (i.e., number of eggs hatched out of a given clutch size) was highest in the high edge density treatment and lowest in the control, but clutch size (i.e., number of eggs in a nest) did not differ among treatments (Appendix S1: Fig. S7, Table 1). The number of nests initiated was higher in the low edge density treatment relative to the control, but...
not relative to the high edge density treatment (Appendix S1: Fig. S7, Table 1). Non-breeding (i.e., winter) survival was higher in the control treatment relative to low or high edge density treatment (Fig. 4B, Table 1). Breeding season survival was lower in the control treatment relative to low or high edge density treatments (Fig. 4B, Table 1). Fecundity tended to be inversely related to non-breeding season survival (Fig. 4C). Bobwhite density (birds/ha) was lower in low edge density treatments relative to the control and the high edge density treatment (Fig. 4D, Table 1). Under the low edge density treatment, bobwhite density was −0.30 birds/ha (95% CI = −0.42, −0.18) lower than the control and −0.37 birds/ha (95% CI = −0.50, −0.25) lower than the high edge density treatment (Table 1). Differences in bobwhite density among treatments were not likely driven by

Fig. 4. Posterior mean and 95% credible limits from our model of northern bobwhite productivity, survival, and density. (A) Fecundity presented as the number of female chicks per female. (B) Season survival presented on the probability scale. (C) Non-breeding season (winter) survival compared to fecundity. (D) Density presented as birds per hectare. Matching letters indicate no significant difference between treatments. A significant difference between treatments means that the 95% credible intervals for the difference in the effect between treatments did not overlap zero.
Table 1. Mean differences and 95% credible intervals among edge density treatments from our models of northern bobwhite productivity, survival, and density.

| Difference       | Mean     | 2.5%  | 97.5% | p   |
|------------------|----------|-------|-------|-----|
| **Productivity** |          |       |       |     |
| Nest.LC          | 0.16     | −0.03 | 0.35  | 0.96|
| Nest.HC          | 0.11     | −0.07 | 0.31  | 0.89|
| Nest.HL          | −0.05    | −0.25 | 0.16  | 0.68|
| Clutch.LC        | 0.34     | −0.66 | 1.33  | 0.76|
| Clutch.HC        | 0.38     | −0.65 | 1.39  | 0.78|
| Clutch.HL        | 0.04     | −0.95 | 1.06  | 0.53|
| Nest. Success.LC | 0.05     | 0.00  | 0.11  | 0.96|
| Nest. Success.HC | 0.11     | 0.05  | 0.17  | 1.00|
| Nest. Success.HL | 0.06     | 0.00  | 0.12  | 0.98|
| Fecundity.LC     | 0.56     | 0.10  | 1.03  | 0.99|
| Fecundity.HC     | 0.67     | 0.17  | 1.19  | 1.00|
| Fecundity.HL     | 0.11     | −0.45 | 0.67  | 0.65|
| **Survival**     |          |       |       |     |
| Survival.CL.B    | −0.11    | −0.22 | 0.00  | 0.98|
| Survival.CH.B    | −0.14    | −0.25 | −0.04 | 0.99|
| Survival.LH.B    | −0.03    | −0.15 | 0.08  | 0.71|
| Survival.CL.NB   | 0.25     | 0.16  | 0.34  | 1.00|
| Survival.CH.NB   | 0.19     | 0.09  | 0.28  | 0.99|
| Survival.HL.NB   | −0.06    | −0.15 | 0.02  | 0.94|
| **Density**      |          |       |       |     |
| Density.LC       | −0.30    | −0.42 | −0.18 | 0.99|
| Density.HC       | 0.07     | −0.04 | 0.20  | 0.81|
| Density.HL       | 0.37     | 0.25  | 0.50  | 1.00|

Notes: Bold values indicate a significant effect (i.e., posterior p value > 0.95).

Results presented as the difference in each vital rate with respect to treatment. For example, Nest.LC, nest initiation in the low and control treatments. Posterior p values (p) represent the proportion of the posterior distribution that was greater than zero. Nests presented as the number of nests per bird. Clutch presented as the clutch size (number of eggs) per nest. Nest success was defined as the proportion of eggs hatched for a given clutch size. Fecundity presented as the number of female chicks per female. Density presented as birds per ha. Abbreviations are: B, breeding season; C, control; L, low; H, high edge density treatment; and NB, non-breeding season.

Differences in movement of individuals among grids. Of the individuals that we tagged and monitored throughout the year, only two permanently moved their territory out of the management unit (250 ha) they were originally captured in.

**DISCUSSION**

Landscapes are increasingly modified for human use, and while many studies explore the effects of losing cover types from landscapes, changes in fragmentation and edge density have received relatively less attention (Pasher et al. 2013, Perović et al. 2015). Experimental studies that provide direct linkages between demography and spatial structure are even rarer (Fahrig 2017). Here, we provide experimental evidence for the impact of spatial structure, specifically edge density, on demography. Winter survival was lower in both low and high edge density treatments, relative to the control. However, in the high edge density treatment, a density-dependent response in fecundity and increased breeding season survival offset negative edge effects, whereas in the low edge density treatment, increased fecundity and breeding season survival were insufficient to offset (along with other possible factors) decreased winter survival, and fall density was lowest in this treatment. Below we discuss the potential mechanisms underlying the relationships we observed, between edge density and demographic rates.

Winter survival was lowest in the low and high edge density treatments. One plausible explanation is that mowing reduces taller vegetation that provides thermal refugia and concealment cover during the winter (Robel and Kemp, 1997). Mortality risk from avian predators could also be contributing to lower winter survival in the edge density treatments. Raptor predation during the fall is a leading cause of mortality among juvenile and adult bobwhite on Tall Timbers and an Albany, Georgia study site (Rectenwald, 2020). Increasing the spatial complexity within our treatment grids involved mowing vegetation, creating avenues for avian predators to use for visually locating prey (Martin and Joron 2003). Density of avian predators was also likely higher during the time of year when mowing occurred (October–November), as this time period precedes annual raptor migration into our study area (January–March; Bohall and Collopy 1984, Rectenwald, 2020). Previous research in other systems has shown a positive relationship between increasing edge density (woody edges, cropland/grassland edges) or decreasing distance to edges, and mortality risk from predation in Galliformes (bobwhites, Seckinger et al. [2008]; ring-necked pheasants, Schmitz and Clark [1999]; turkeys, Thogmartin and Schaeffer [2000]).

Contrary to our density-independent prediction (Fig. 1), fecundity was lower in the control, relative to areas with some amount of linear...
edge. One explanation could be a density-dependent response in productivity, with a decline in the number of individuals surviving to the breeding season (McConnell et al. 2018). Indeed, the negative relationship we observed between fecundity and winter survival suggests a negative density-dependent response in fecundity (Rodenhouse et al. 2003). If resources (e.g., space, cover) are limiting productivity in our population, a lower survival rate in the low edge density treatment relative to the control could mean more resources for a lower density of adults alive at the onset of the breeding season (Skogland 1985, Arcese and Smith 1988, Rodenhouse et al. 2003). Consequently, those adults may have more resources to invest in breeding, resulting in a higher number of chicks produced per hen. In forest-dependent bird species, fragmented habitat patches with higher population densities have been shown to have lower pairing success and productivity (Hagan et al. 1996). There are currently no studies investigating the influence of density on chick production in bobwhite, and so this remains an area for future research. Another possible explanation relates to the predator assemblage, with respect to edge density treatments. Potential bobwhite nest predators (e.g., snakes and mesomammals) moving through the lanes created by mowing during the non-breeding season could be experiencing higher rates of predation themselves, relative to the control landscapes during the breeding season. This hypothesis is supported by the higher proportion of eggs hatched (i.e., nest success) in landscapes with linear edge, relative to the control landscapes. A decrease in the density of potential nest predators during autumn (i.e., snakes, mesomammals) may be leading to an increase in nest success during spring (Staller et al. 2005). It is also possible that winter mowing reduces hardwood sprouts in the short term (Pierce et al. 2005). Combined with burning that occurs during the spring, these management practices may lead to an increase in herbaceous vegetation during the breeding season and subsequently more energy available to breeding individuals for chick production (Peitz et al. 1997).

The relationship between survival and edge density was reversed in the breeding season, with birds in the control experiencing a lower survival rate relative to the edge density treatments. Similar to differences in fecundity we observed among treatments, it is plausible that the differences in survival rate were a density-dependent response. For example, if resources are limiting, a higher density of individuals entering the breeding season in the control treatments could lead to a lower breeding season survival rate (Frederiksen and Bregnballe 2000). Density-dependent survival rates have been observed in other avian populations (Armstrong et al. 2002, Marra et al. 2015). Previous studies of bobwhite survival conducted in our study system provided evidence that annual survival declined as population density increased (McConnell 2016). However, McConnell (2016) did not decompose survival into breeding and non-breeding seasons. Alternatively, predation rates may be density-dependent such that as bobwhite densities increase, so do mortality rates (e.g., Whitfield 2003). In previous studies, the primary cause of bobwhite mortality during the breeding season was predation (Taylor et al. 1997, Sisson et al. 2009), specifically predation by mammals and birds, as well as snake predation on chicks (Lunsford et al. 2019). Furthermore, as bobwhite population densities increased, so did predation rates from avian predators (Taylor et al. 1997). Estimates of spring population densities would help determine whether the decline in breeding season survival in the control quadrats was in response to higher seasonal population densities, or whether it was more a direct response to an increase in herbaceous vegetation stimulated by mowing (Peitz et al. 1997).

Our experiment contributes to a growing body of ecological research evaluating the effects of landscape pattern on population dynamics. We hypothesize that in the high edge density treatment, a decline in winter survival may have been offset by a density-dependent response in fecundity and breeding season survival (Rodenhouse et al. 2003). However, populations in other study systems may not experience a density-dependent response in fecundity. Fecundity may not be limited by competition for resources during the breeding season (i.e., food, space). In these situations, reducing crowding will not increase access to higher quality habitat and no density-dependent response in fecundity would be predicted. It is also possible that the reduction in habitat amount and increase in edge may reduce the
quality of nesting habitat to the point that the landscape is insufficient to facilitate a density-dependent fecundity response. In these cases, the recommendation may be to maintain contiguous landscapes with no internal edges and avoid reducing survival. Alternatively, managers could intersperse un-fragmented landscapes with some landscapes containing a higher density of moved edges. This type of landscape mosaic management strategy may be effective for providing adequate habitat for grassland birds in fragmented landscapes, while also providing access for recreation.

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**DATA AVAILABILITY**

Data and code are available from Figshare: https://doi.org/10.6084/m9.figshare.12009228.v1.

**SUPPORTING INFORMATION**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3499/full