RESEARCH ARTICLE

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

Private land conservation has landscape-scale benefits for wildlife in agroecosystems

John M. Yeiser[1] | John J. Morgan[2] | Danna L. Baxley[2] | Richard B. Chandler[1] | James A. Martin[1]

[1]Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA

[2]Kentucky Department of Fish and Wildlife Resources, Frankfort, KY, USA

Correspondence
John M. Yeiser
Email: yeisjohn@gmail.com

Funding information
Kentucky Department of Fish and Wildlife Resources; Federal Aid to Wildlife Restoration Act (Pittman–Robertson); University of Georgia

Handling Editor: Danny Hooftman

Abstract

1. Private lands contain much of the world's biodiversity. Conservation of private land, especially agricultural land, is urgent yet challenging because of the diverse priorities of landowners. Local effects of farmland conservation programmes have been evaluated thoroughly, but population-level response to these programmes may depend on effects that extend beyond targeted land parcels. We investigated the landscape-scale effects of a grassland conservation initiative, the Conservation Reserve Enhancement Program (CREP), on a socially and economically important game bird, the Northern Bobwhite *Colinus virginianus*.

2. Barriers to assessing population-level response to conservation include determining the spatial scale at which a species responds to environmental change (the scale of effect) and untangling density-dependent processes. We performed point counts over 6 years at 247 sites with similar local CREP density but varying landscape-scale CREP density. We used an open-population distance sampling model to evaluate population response to landscape-level CREP density and to forecast population densities under differing re-enrolment scenarios. Our model included kernel smoothing techniques to estimate scale of effect and an estimator of the strength of density dependence.

3. Density dependence moderated the effectiveness of the CREP, but overall populations responded positively to increasing landscape-scale CREP density. We estimated that at least 5% of the landscape needs to be in CREP to meet population density goals of 0.25 bobwhite/ha. Conservatively, we recommend 10% of the landscape to be in CREP. Our percent cover recommendations are based on a distance-weighted average of CREP around focal sites.

4. Landscape-scale effects diminished with distance. For example, assuming all else is equal, a CREP field 3,000 m away had 88% less of an effect on local abundance than a field 1,000 m away. Fields farther than 5,000 m away had no effect on local abundance.

5. *Synthesis and applications*. Our study underscores the importance of a landscape-scale approach to farmland conservation. Benefits of these programmes to wildlife can extend beyond the local scale, but their importance to local populations

diminishes with distance. Estimating this relationship and incorporating it into a decision framework could help practitioners target land enrolment to meet broad-scale population objectives.

1 | INTRODUCTION

Government policy can establish guidelines or goals for wildlife conservation, but on-the-ground implementation over broad-spatial scales is complicated by the different priorities of landowners and varying opportunities for conservation delivery (Morgan, Sprandel, Robinson, & Wethington, 2012; Paloniemi & Tikka, 2008). Balancing effective policies and agricultural land use is a formidable challenge for conservation around the world (Tscharntke, Clough, et al., 2012), especially in areas where the majority of land is privately owned. For example, the commonwealth of Kentucky is 96.5% privately owned and approximately half of that is agricultural land. In spite of the challenges, private land conservation is urgently needed because agriculture has driven declines of imperiled species such as grass-land birds (Donald, Green, & Heath, 2001; Murphy & Moore, 2003).

Private land conservation programmes such as agri-environmental schemes (AES) and the Conservation Reserve Program (CRP) are used throughout Europe and United States, respectively, to mitigate farmland bird population declines. The CRP is a US Department of Agriculture programme administered by the Farm Service Agency that incentivizes landowners to temporarily remove agricultural land from production in lieu of an approved conservation practice. Similar to set-aside programmes within AES, the CRP can be viewed as a form of land sparing (Fischer et al., 2008). Fields enrolled in grassland CRP practices are typically higher quality habitat for grassland birds than active agriculture (Best et al., 1998; Johnson & Schwartz, 1993). Although localized positive effects of CRP and similar conservation programmes are well documented (e.g. Buckingham, Evans, Morris, Orsman, & Yaxley, 1999; Halloum, Leo, & Heard, 2000), the effectiveness of private land conservation in reversing grassland bird declines is tied to landscape-scale effects (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011), that is, the geographic extent of conservation benefits beyond targeted land parcels. Landscape-scale studies directly modelling the impacts of conservation on population growth are less common (but see Baker, Freeman, Grice, & Siriwardena, 2012; Riffell, Scognamillo, & Burger, 2008; Veech, 2006). Conservation in agricultural landscapes should be designed to benefit multiple populations (or subpopulations or communities) simultaneously, yet there is little congruence in what constitutes a landscape for grassland birds (Osborne & Sparling, 2013; Pabian, Wilson, & Brittingham, 2013; Riffell et al., 2015).

The mechanisms driving the spatial scale at which a species is most responsive to environmental change (the scale of effect) include a species' traits (e.g. mobility), demography (e.g. reproductive rate) and landscape characteristics (e.g. matrix quality), and these mechanisms may vary regionally (Miguet, Jackson, Jackson, Martin, & Fahrig, 2016). Thus, determining the scale of effect of a conservation programme on wildlife is a necessary step to understanding population-level response (Smith, Fahrig, & Francis, 2011; Wiens, 1989). One way to determine scale of effect is to use the focal patch approach, in which independent variables within several nested landscapes are related to dependent variables measured at local sites (Brennan, Bender, Contreras, & Fahrig, 2002). This method reduces uncertainty about appropriate spatial scales but can produce spurious scale selection (Jackson & Fahrig, 2015), implicitly ignores theories of how populations and individuals interact with landscapes such as optimal foraging theory (Charnov, 1976) and metapopulation dynamics (Hanski & Gilpin, 1991) and ignores uncertainty about chosen scale of effect. An alternative approach is to estimate the scale of effect using smoothing kernels to acknowledge that the importance of a landscape feature should decline with distance to the focal site (Chandler & Hepinstall-Cymerman, 2016). Understanding the relationship between the importance of a resource patch and distance to a local population is critical to effective private land conservation over broad scales (Whittingham, 2007), and this relationship can directly inform conservation planning by defining species-specific landscapes (Supporting information).

Just as population response to conservation varies across space, population performance in response to conservation measures will vary with time as intrinsic factors such as density-dependence manifest. Modelling population dynamics usually requires information on marked individuals (e.g. Pradel, 1996); however, spatially and temporally replicated counts can be sufficient to estimate population growth rates (Dail & Madsen, 2011; Royle, 2004). Modelling growth allows us to use classical population models that do not assume resources are unlimited (Hostetler & Chandler, 2015; Nadeem, Moore, Zhang, & Chipman, 2016). Realistic growth models facilitate population forecasting and allow us to compare the ramifications of alternative management scenarios. Understanding potential population response to alternative conservation strategies is especially relevant to the CRP because landowner contracts are temporary and resource management agencies have finite political, monetary and logistical capital to dedicate to re-enrolment efforts. Thus, we need biologically realistic models to understand the uncertainty surrounding the response of populations to differing re-enrolment strategies.

In agricultural landscapes, grassland bird populations are driven by resource availability (Butler, Boccaccio, Gregory, Vorisek, & Norris, 2010), specifically food and nesting resources (Benton, Bryant, Cole, & Crick, 2002; Butler, Vickery, & Norris, 2007). Assuming that increased amount of nesting habitat would result in increased net reproductive output (Sutherland, 1996), we would expect individual fitness and population growth to increase in response to a grassland conservation programme (Matthiopoulos et al., 2015). Particularly, we would expect the population response to outweigh the conservation footprint (i.e. a 10% increase in high quality nesting habitat would result in more than a 10% population increase), especially if additional nesting habitat complements existing resources (Dunning, Danielson, & Pulliam, 1992). However, if nesting resources are not complementary to other resources, we may expect to see a nonlinear trend in abundance in our first year of sampling across the gradient of conservation land density as other resources become limiting. Alternatively, if nesting resources are not the main factor limiting a grassland-associated species (e.g. Janke & Gates, 2013), implementing a grassland conservation programme would merely supplement existing resources (Dunning et al., 1992) and would initiate a response proportional to conservation footprint. Under any of these scenarios, density-dependent processes may manifest over time as population density increases (Roseberry & Klimstra, 1984).

Our goal was to investigate the population-level effects of implementing a grassland conservation programme. We used the Kentucky Conservation Reserve Enhancement Program (CREP) as a model conservation programme and Northern Bobwhite (*Colinus virginianus*, hereafter: bobwhite) as a model species. We chose bobwhite because the adoption of high efficiency "clean farming" has contributed to their exacerbated declines (reviewed in Hernández, Brennan, DeMaso, Sands, & Wester, 2013), and they are a socially and economically valuable game bird. The CREP is an offshoot of the CRP that allows eligible states to define specific conservation priorities. Practices implemented for the CREP are based on CRP practices, but landowner eligibility requirements are often more stringent. Our objectives were to (1) estimate the spatial scale at which bobwhite respond to private land conservation, (2) model the response of bobwhite population density and growth to increasing landscape-scale CREP density, while holding local CREP density constant, and (3) project populations under varying levels of CREP re-enrolment, concurrent with contract expiration dates, up to 25 years beyond the starting point of our study.

We had three competing hypotheses about how bobwhite populations would respond to the CREP soon after programme implementation, and these hypotheses were based on the assumption that CREP was primarily providing nesting resources. We hypothesized that bobwhite would display (1) a positive response that outweighs conservation footprint and does not diminish along the CREP density gradient (resource complementation hypothesis) or (2) a positive response that outweighs conservation footprint yet diminishes as conservation land density reaches high densities (nesting resources only hypothesis) or (3) a positive response directly proportional to conservation footprint (nesting resource supplementation hypothesis). We also hypothesized that population growth would display negative density dependence because bobwhite are thought to be regulated via a reduction in survival or recruitment (Errington, 1945; Roseberry & Klimstra, 1984).

2 | MATERIALS AND METHODS

We studied the influence of the CREP on bobwhite in the Green River Basin in south central Kentucky during 2010–2015 (Supporting information). Annual high temperatures average 20.5°C, with average highs in November–February, March–May, June–August and September–October of 10.3, 20.7, 31.1 and 24.7°C respectively. Average annual precipitation is 126.2 cm. The Green River Basin is characterized by karst topography with elevation ranging from 91 to 365 m above sea level. The Kentucky CREP consisted of several conservation practices (Supporting information), although the majority were CP29 (Marginal Pastureland Wildlife Buffer, 71%) and CP22 (Riparian Buffer, 16%). Although CP29 is described as a buffer, whole fields were enrolled and planted in mostly short grass prairie mixes. The CP22 fields were primarily a row of planted hardwoods with extended buffers seeded in tallgrass prairie mixes. The majority of contracts were initiated in 2008; thus, our initial year of sampling (2010) was at least one growing season after most fields had been planted.

We used a stratified random sampling design (Supporting information). We assumed that a 3,000 m radius circle was an appropriate landscape scale to inform study design (Twedt, Wilson, & Keister, 2007); however, our statistical methods directly test this assumption. We randomly selected sampling points within each of five CREP density strata (Supporting information), and point selection was informed by a power analysis. Kentucky Department of Fish and Wildlife Resources biologists performed 5-min distance sampling point counts at each site for 6 years during the month of June. Observers typically surveyed the same points each year; however, some points went unsampled in 2010. We truncated bobwhite detection distances to 450 m and aggregated detections by distance bands based on the recommendations of Buckland (2001).

We fit the data to an open-population distance sampling model (Royle, Dawson, & Bates, 2004; Sollmann, Gardner, Chandler, Royle, & Sillett, 2015). These models have three main components: (1) a model for initial abundance, (2) a model for abundance in subsequent years $t = 2...T$ and (3) detection conditional on abundance. We modelled initial abundance at each site $\mathbf{x}_i$ using a negative binomial distribution, where expected abundance $\lambda(\mathbf{x}_i)$ varied with linear and quadratic landscape-scale CREP density. We allowed initial abundance to vary with local CREP density, although our study design rendered relatively low variation in local CREP density:

$$\log(\lambda(\mathbf{x}_i)) = \alpha_0 + \alpha_1 \text{CREP}(\mathbf{x}_i) + \alpha_2 s(\text{CREP}(\mathbf{x}_i), \sigma_{\text{CREP}}) + \alpha_3 s(\text{CREP}(\mathbf{x}_i), \sigma_{\text{CREP}})^2$$

$$N(\mathbf{x}_{i,1}) \sim \text{NegBin}(\lambda(\mathbf{x}_i), r)$$

where α_0 is the intercept, α_1 is the effect of local CREP density, α_2 is the linear effect of landscape-scale smoothed CREP density, α_3 is the quadratic effect of landscape-scale smoothed CREP density and r is an estimate of overdispersion in counts. We modelled abundance in subsequent years using a Poisson distribution, with expected density a product of abundance in the previous year and a population growth rate. We chose a Poisson distribution based on preliminary assessments of Bayesian p-values. Our model combines elements of the Dail–Madsen model (Dail & Madsen, 2011) into one growth rate, γ. As $N(\mathbf{x}_{i,t})$ is tied to $N(\mathbf{x}_{i,t-1})$, estimating γ alone does not account for immigration following local extinction, which can superficially deflate detection probabilities and overestimate abundance. Thus, we modelled an immigration rate I separate from γ. Therefore, γ represents the results of survival, recruitment and emigration and I represents immigration, and together they represent overall population growth at site $\mathbf{x}_i$ from year $t - 1$ to year t. We assumed γ and I to be constant among years, yet overall growth rate could vary based on density-dependent processes:

$$\gamma(\mathbf{x}_{i,t}) = N(\mathbf{x}_{i,t-1}) \exp(\theta_0 + \theta_1 N(\mathbf{x}_{i,t-1}) + \theta_2 \text{CREP}(\mathbf{x}_i) + \theta_3 s(\text{CREP}(\mathbf{x}_i), \sigma_{\text{CREP}}))$$

$$I(\mathbf{x}_{i,t}) = \exp(\iota_0 + \iota_1 s(\text{CREP}(\mathbf{x}_i), \sigma_{\text{CREP}}))$$

$$N(\mathbf{x}_{i,t}) \sim \text{Poisson}(\gamma(\mathbf{x}_{i,t}) + I(\mathbf{x}_{i,t}))$$

where θ_0 is intrinsic γ, θ_1 is the strength of density dependence on γ, θ_2 is the influence of site-level CREP density on γ, θ_3 is the influence of landscape-scale smoothed CREP density on γ, ι_0 is the intercept of immigration rate and ι_1 is the effect of landscape-scale smoothed CREP on immigration rate. For each year in our model, we used a half-normal key function to estimate the probability of detecting a singing individual in each distance band, and observations were modelled using a multinomial distribution (Supporting information).

We smoothed landscape-scale CREP by aggregating our input raster to cell sizes approximately equal to our sampling units (63 ha) and produced a distance-weighted average of CREP density at each cell using the spatial smoother examined in Chandler and Hepinstall-Cymerman (2016):

$$s(\text{CREP}(\mathbf{x}_i), \sigma_{\text{CREP}}) = \sum_{(\mathbf{x}_j \neq \mathbf{x}_i) \in S} \text{CREP}(\mathbf{x}_j) w(\mathbf{x}_i, \mathbf{x}_j, \sigma_{\text{CREP}})$$

where weights $w(.)$ are determined by a Gaussian kernel:

$$w(\mathbf{x}_i, \mathbf{x}_j, \sigma_{\text{CREP}}) = \frac{\exp(-\|\mathbf{x}_i - \mathbf{x}_j\|^2)/(2\sigma_{\text{CREP}}^2))}{\sum_{(\mathbf{x}_j \neq \mathbf{x}_i) \in S} \exp(-\|\mathbf{x}_i - \mathbf{x}_j\|^2)/(2\sigma_{\text{CREP}}^2))}$$

where $|\mathbf{x}_i - \mathbf{x}_j|$ is the Euclidean distance between coordinates of pixel i and pixel j, and σ_{CREP} is the estimated scale parameter that dictates the shape of the Gaussian kernel. The summation does not include the pixel of interest "i" because we are interested in the effect of the surrounding landscape on local abundance. We restricted the search area of the Gaussian kernel to a 10 km radius circle to reduce computational effort. We assumed a 10 km radius circle would easily encompass the maximum scale of effect for bobwhite.

We modelled data from 2010 to 2015 and forecasted populations for 20 additional years under six different scenarios: 100%, 80%, 60%, 40%, 20% and 0% CREP re-enrolment. For each scenario each year, we randomly selected a percentage of contracts set to expire and "re-enrolled" them. We assumed detection in the years 2016–2035 was a random draw from a normal distribution with mean and standard deviation informed by estimates from the years (2010–2015) with data. To quantify the probability that one scenario would result in higher densities than another, we calculated the integral of overlap between any two posterior distributions of estimated densities in 2035.

We ran each model scenario in a Bayesian framework using the Markov Chain Monte Carlo algorithm in JAGS (Plummer, 2003) with the R package rjags (Plummer, 2016). We discarded the adaptive phase and appropriate number of iterations for each scenario to remove the influence of starting values. We ensured model convergence using Gelman–Rubin diagnostics and visual inspection of trace plots. Model code for rjags is included in the Supporting information.

3 | RESULTS

We sampled 231 points in 2010 and 247 points from 2011 to 2015. We detected 159, 182, 180, 195, 227 and 180 male singing bobwhite in 2010–2015 respectively. We estimated detection probabilities for the years 2010–2015 to be 0.35 (0.28–0.43, 95% BCI), 0.33 (0.29–0.39), 0.33 (0.29–0.37), 0.31 (0.27–0.35), 0.33 (0.29–0.38), 0.30 (0.25–0.34) respectively.

Bobwhite landscapes were delineated at c. 5,000 m radius circles. The importance of CREP density to a local bobwhite population decreased with increasing distance (Figure 1). For example, the median weight of a pixel (i.e. a cell in the covariate raster) 3,000 m away from a local population was 88% lower than a pixel 1,000 m away.

There was a 99.3% probability of a positive effect of landscape-scale CREP density on initial bobwhite density (Figure 2). Bobwhite densities in the initial year of sampling ranged from 0.016 (0.009–0.025, 95% BCI) to 0.056 males/ha (0.006–0.162, 95% BCI) across the landscape-scale CREP density gradient. The response of initial bobwhite density to the CREP was consistent with our "nesting habitat only" hypothesis. An increase from 0.0 to 0.1 landscape-scale CREP density resulted in a 182% increase in bobwhite density. However, an increase from 0.1 to 0.2 landscape-scale CREP density resulted in only a 21% increase in bobwhite density (Figure 3).

There was a 95.2% probability that γ (the result of survival, recruitment and emigration) was positively influenced by landscape-scale CREP density (Figure 2). There was a 89.6% probability that I (immigration) was positively influenced by landscape-scale CREP density (Figure 2). We estimated that negative density dependence on γ was c. 8% of the previous year's abundance. Overall
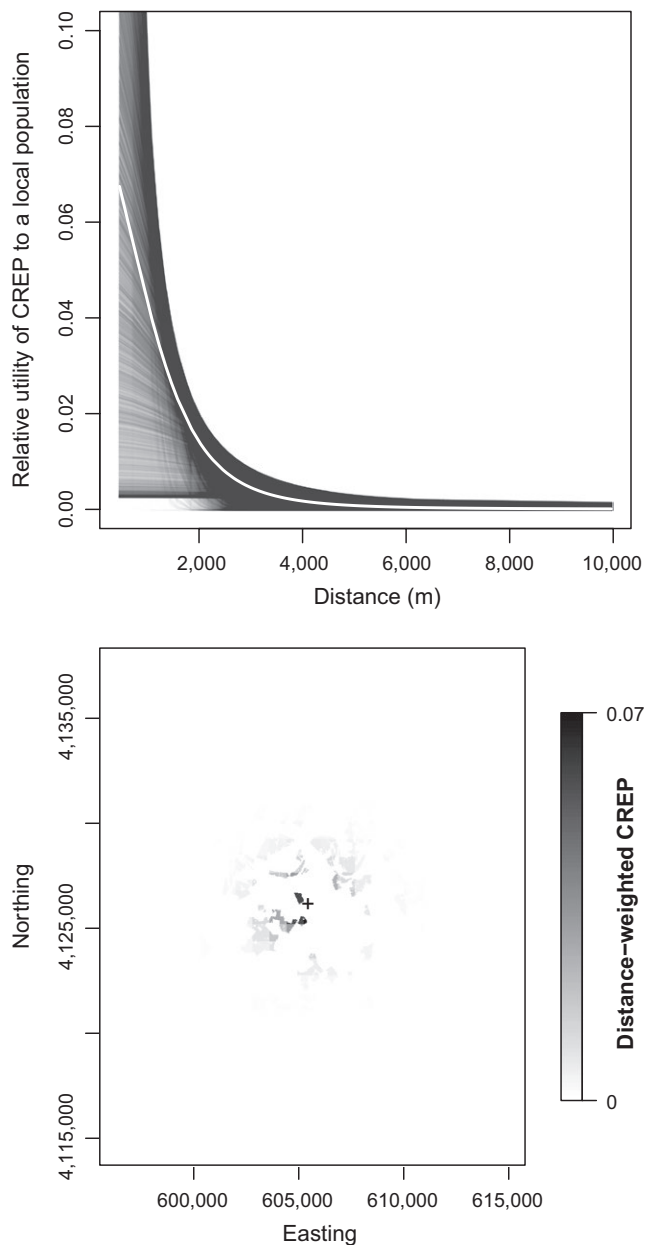
FIGURE 1 Top: the relationship between distance and the relative utility of Conservation Reserve Enhancement Program (CREP) density to a local Northern Bobwhite (*Colinus virginianus*) population in south central Kentucky (the scale of effect). The y-axis represents Gaussian kernel weights of a given pixel (i.e. a 63 ha area) relative to all pixels in a 10 km radius search area (31,416 ha). Higher values reflect distances at which increases in CREP density are more likely to influence the local population. Each black line represents one of 10,000 randomly chosen model iterations. The solid white line represents the median estimate. Bottom: a visual representation of how Northern Bobwhite experience landscapes in south central Kentucky. The "+" symbol represents a local population, and the black polygons represent CREP fields. The degree to which each field is shaded represents the relationship between increasing distance and relative utility of a that field to the local population abundance and growth rate

population growth mirrored conservation footprint at low amounts of landscape-scale CREP but outweighed conservation footprint at high amounts of landscape-scale CREP (Figure 4). Densities in our final year of sampling (2015) ranged from 0.034 (0.024–0.046, 95% BCI) to 0.105 males/ha (0.063–0.159, 95% BCI).

We predicted that re-enrolling 80%, 60%, 40%, 20% and 0% would result in mean densities 10%, 19%, 26%, 33% and 39% lower than if 100% of contracts were re-enrolled respectively (Figure 5). Our forecasts indicated a 32%, 57%, 71%, 81% and 87% probability that re-enrolling 100% of CREP contracts would lead to higher densities in the year 2035 than 80%, 60%, 40%, 20% and 0% re-enrolment respectively.

4 | DISCUSSION

Agricultural landscapes—and thus resources added by farmland conservation programmes—are inherently patchy. Understanding whether benefits of conservation extend beyond local scales is paramount to assessing the population-level success of farmland conservation programmes (Kleijn et al., 2011). We found evidence that (1) farmland conservation benefits population growth via landscape-scale effects, (2) landscape-scale effects decrease with increasing distance to a local population, (3) density-dependent growth moderates population response and (4) long-term success will be tied to re-enrolment effort.

Translating local effects of farmland conservation programmes to scales meaningful to populations is a challenge to successful regional-scale conservation. Donald and Evans (2006) noted that benefits of farmland conservation programmes could extend beyond local scales via metapopulation dynamics and mechanisms of island biogeography theory; however, evidence for landscape-scale benefits to bird populations is sparse. Baker et al. (2012) demonstrated how AES can have landscape-scale positive effects on birds in England, but regional-scale assessments of the CRP have not explicitly considered the effects of increasing conservation land density in the surrounding landscape on population growth (Riffell et al., 2008; Veech, 2006). Our results demonstrate that the amount of conservation land in the surrounding landscape affects local population dynamics. This underscores the importance of the landscape-scale approach to farmland conservation (e.g. Merckx et al., 2009).

The nonlinear relationship between bobwhite density and landscape-scale CREP density in 2010 could reflect an ecological threshold. Increased amount of landscape-scale CREP likely resulted in increased landscape complexity (Fahrig, 2003). Benefits of landscape complexity include increased dispersal capabilities as a result of high connectivity and increased complementation of resources as a result of land cover configuration (Concepción et al., 2012). We would expect that in landscapes with high CREP density (complex landscapes), CREP fields would be closer to existing brood
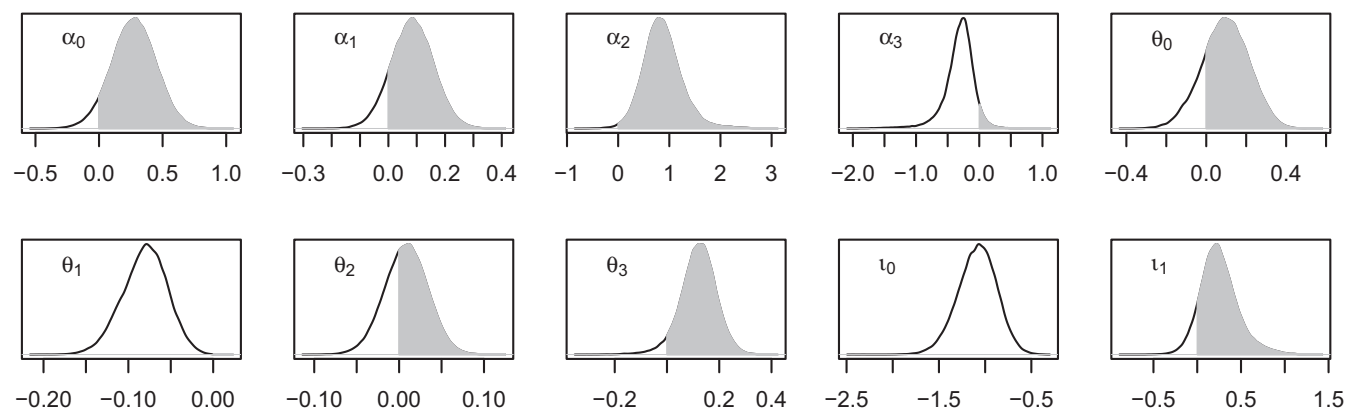
FIGURE 2 Posterior densities of parameters describing the response of Northern Bobwhite *Colinus virginianus* to Conservation Reserve Enhancement Program (CREP) density. Shaded areas represent the proportion of posterior mass greater than zero for: (α_0) the intercept of abundance in our first year of sampling (initial abundance); (α_1) local effect of CREP density on initial abundance; (α_2) landscape-scale linear effect of CREP density on initial abundance; (α_3) landscape-scale quadratic effect of CREP density on initial abundance; (θ_0) the intercept of γ (the combined rates of survival, recruitment and emigration); (θ_1) effect of local population abundance on γ; (θ_2) local effects of CREP density on γ; (θ_3) landscape-scale effects of CREP density on γ, (ι_0) intercept of immigration and (ι_1) landscape-scale effects of CREP density on immigration
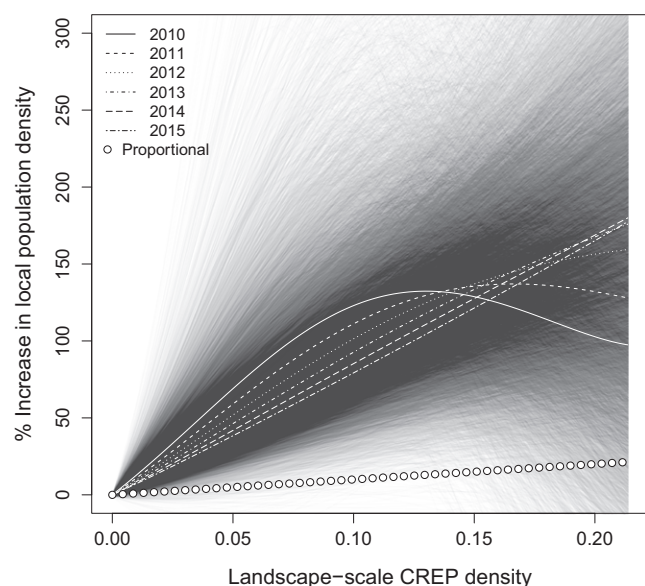
FIGURE 3 Magnitude of response of Northern Bobwhite *Colinus virginianus* density to increasing landscape-scale Conservation Reserve Enhancement Program (CREP) density in the years 2010–2015. Each black line is one iteration in the MCMC algorithm and white lines represent means for each year. The circles reference a proportional response to a one unit increase in landscape-scale CREP density

FIGURE 4 Magnitude of response of Northern Bobwhite *Colinus virginianus* population growth to increasing landscape-scale Conservation Reserve Enhancement Program (CREP) density in the years 2010–2015. Each black line is one iteration in the MCMC algorithm and white lines represent means for each year. The circles reference a proportional response to a one unit increase in landscape-scale CREP density

rearing cover, thermal cover and escape cover relative to landscapes with low CREP density, which would have complementary benefits to bobwhite populations (Dunning et al., 1992; Guthery, 1997). Tscharntke, Tylianakis, et al. (2012) reviews evidence for an upper threshold after which increased landscape complexity no longer benefits biodiversity (20% habitat amount). The inflection point in the nonlinear relationship we observed occurred before 20% CREP
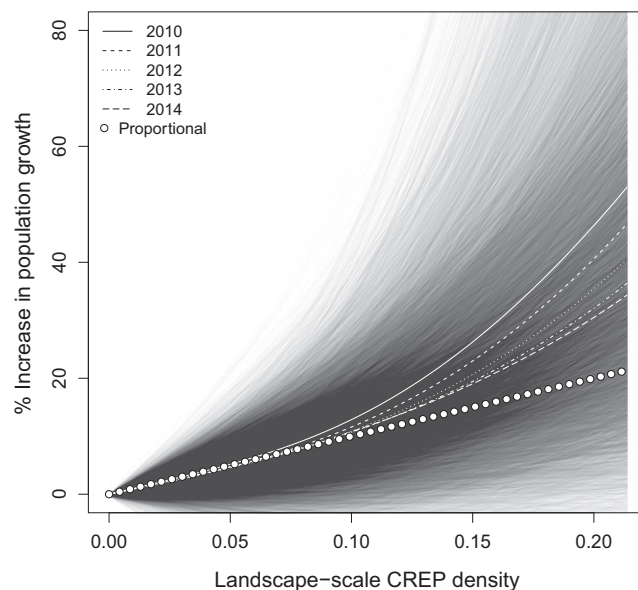
density, which suggests that the resources provided to bobwhite by CREP fields do not reflect total habitat amount.

Alternatively, the nonlinear response of bobwhite abundance to increasing landscape-scale CREP density in 2010 could reflect the composition, not configuration, of resources in landscapes. A major resource that limits bird populations in farm landscapes is nesting cover (Benton et al., 2002; Butler et al., 2007). Fields planted in warm season grasses and forbs (e.g. CREP fields) provide ample
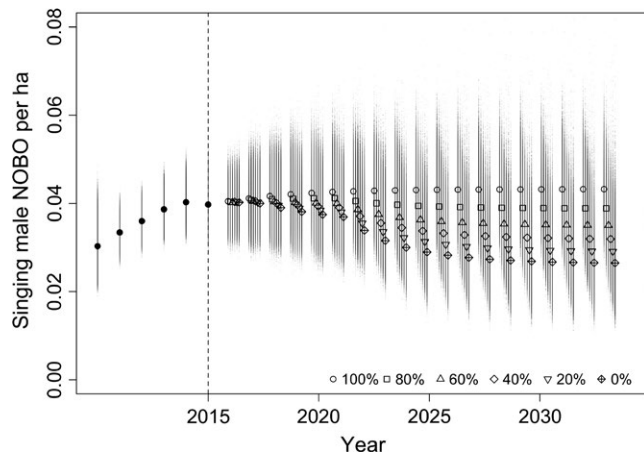
FIGURE 5 Projected mean densities of Northern Bobwhite *Colinus virginianus* populations under different re-enrolment scenarios for the Conservation Reserve Enhancement Program. Error bars are composed of point estimates from each model iteration

nesting sites for bobwhite (Washburn, Barnes, & Sole, 2000), but unless frequently and appropriately disturbed, openness at ground level and quality of brood rearing cover diminishes (e.g. Yeiser, Baxley, Robinson, & Morgan, 2015). Additionally, it was unlikely that the CREP provided thermal or escape cover in 2010 because landowners planted woody cover infrequently. If we assume that bobwhite populations are indeed limited by resources that they require but are not readily available (Taylor, 1934), the nonlinear trend in 2010 could reflect other resources-limiting populations after nesting resources are sufficiently dense. Thresholds are typically discussed in terms of total habitat amount (e.g. Swift & Hannon, 2010), but the management of wildlife populations may benefit from estimating inflection points in the profile of resources that are limiting population growth.

The regulation of population growth by population density in bobwhite during our study was consistent with the idea that density dependence is an elemental feature of population dynamics (Brook & Bradshaw, 2006). Carrying capacity is influenced by the availability of resources and the use of those resources by individuals within the population, intra- and interspecific competition and predators (del Monte-Luna, Brook, Zetina-Rejón, & Cruz-Escalona, 2004). Similar to Baker et al. (2012), we demonstrated that by increasing a limiting resource (nesting cover), we can increase the carrying capacity of landscapes. Our results also suggest that increasing carrying capacity further may require conservation programmes to provide a variety of resources to the species or taxa of interest, which underscores the importance of a functional approach to private land conservation. Inventory of existing resources via remote sensing, evaluation of freely available land cover data (e.g. National Land Cover Database) and expert opinion could facilitate an understanding of the functional quality of landscapes (Fahrig et al., 2011) and inform future private land conservation priorities.

Recent literature advocates for goal-oriented, spatially targeted farmland conservation (e.g. Batáry, Dicks, Kleijn, & Sutherland, 2015; Díaz & Concepción, 2016; Whittingham, 2007). Spatially targeted conservation intended to optimize biodiversity, species abundance or species occurrence requires an understanding of landscape context because landscape factors influence population structure and dynamics (Tscharntke, Tylianakis, et al., 2012). An implicit assumption of spatial targeting, then, is that we know the appropriate landscape scale. Landscapes are species-specific concepts (Jackson & Fahrig, 2012), and the likelihood that a population will utilize resources added by farmland conservation will be moderated by its distance to those resources (Whittingham, 2007), with the assumption being that resources closer to the focal population are more likely to be utilized (Charnov, 1976; Hanski & Gilpin, 1991). Consequently, understanding species-specific forms of the relationship between increasing distance and the utility of resources would facilitate spatially targeted conservation. The kernel smoother we used is tractable and can be implemented in many modelling scenarios (Chandler & Hepinstall-Cymerman, 2016); thus, when empirical data are available, it is a powerful framework for spatial optimization. However, if empirical data are unavailable during conservation planning, we recommend using potential mechanisms of species-specific scales of effect (e.g. Miguet et al., 2016) to hypothesize appropriate landscape boundaries and to predict the shape of the relationship between resource utility and increasing distance (e.g. half-normal or negative exponential). Subsequent monitoring and modelling similar to what we present herein could be used to establish an adaptive management framework that continually informs planning decisions.

The enrolment strategy of the CREP was to simply implement 40,468 ha of conservation land. There was no consideration of landscape structure or ecological connectivity. Is this opportunistic approach a viable private land conservation strategy? The National Bobwhite Conservation Initiative (NBCI) established density goals for Kentucky of 0.25 bobwhite/ha in the non-breeding season in pasture-dominated landscapes (National Bobwhite Technical Committee, 2011). If we use our last year of data (2015), assume all singing males paired with a female, singing males represented the entire breeding male population and use a conservative estimate of overwinter survival (0.40), non-breeding season densities in 2014 ranged from 0.17 (0.12–0.24, 95% BCI) to 0.48 (0.34–0.67, 95% BCI) across the landscape-scale CREP gradient. The landscape would need to have at least 5% (1%–10%, 95% BCI) CREP cover to produce 0.25 bobwhite/ha. Conservatively, we recommend practitioners aim for 10% grassland land cover in the landscape surrounding focal sites to reach this goal. These percent cover recommendations are weighted by distance. Evaluating the amount of grassland land cover in any given landscape will require accounting for its configuration, specifically distances between grassland fields and the focal site.

Our forecasts indicate that the ultimate factor dictating long-term success of the CREP in Kentucky will be re-enrolment effort. By presenting forecasted outcomes of alternative management scenarios, we have provided resource management agencies with information that could aid prioritization of re-enrolment of CREP

in Kentucky. First, prioritization should be rooted in conservation outcomes, for example, meeting or maintaining NBCI density goals for bobwhite. Managing landscapes for bobwhite may be the most practical way to conserve grassland bird biodiversity in the Eastern US, as bobwhite can be an umbrella species for other grassland and shrubland birds (Crosby, Elmore, Leslie, & Will, 2015) and their importance to sportsmen and women often drive farmland conservation policy (e.g. Conservation Practice 33). Second, agencies could use our forecasts to understand opportunity costs of different management decisions. For example, is the increased cost of re-enrolling 100% of contracts vs. 80% of contracts worth the potential gain in bobwhite density, given that there is only a 32% probability of obtaining greater densities? Finally, spatial prioritization could be guided by the estimated relationship between increasing distance and utility of CREP fields to local populations. Simulations quantifying the potential differences in carrying capacities resulting from random, opportunistic and spatially targeted re-enrolment at some percentage (e.g. 80%) are necessary to fully inform these decisions, and we believe our modelling framework is a first step in that process. The development of user-friendly, data-driven decision support tools that allow spatially explicit value inputs such as population goals, monetary and logistical resources, and landowner interest would facilitate the transfer of research findings and policy objectives to on-the-ground conservation.

Our study is an example of how outcome-based monitoring contributes to strategic habitat conservation and provides guidance on the practical considerations of employing a landscape-scale approach to farmland conservation. Specifically, we expect our findings to have implications for planning and implementation of CRP and CREP in the U.S. and similar voluntary set-aside practices across Europe. We believe the advancement of knowledge on (1) how and why landscape scales vary among and within species, (2) functional relationships between population growth and land cover composition and landscape context and (3) repercussions of spatially targeted land enrolment vs. random or opportunistic enrolment would improve the efficiency of farmland conservation.

AUTHORS' CONTRIBUTIONS

J.M. and D.B. conceived and designed the study. J.Y. conducted the analysis, interpreted the data and was the primary author of this manuscript. R.C. and J.M. contributed to the analysis and interpretation of data and development of statistical models. All authors contributed to revisions of draft manuscripts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.bn7p2f5 (Yeiser, Morgan, Baxley, Chandler, & Martin, 2018).

REFERENCES

Baker, D. J., Freeman, S. N., Grice, P. V., & Siriwardena, G. M. (2012). Landscape-scale responses of birds to agri-environment management: A test of the English Environmental Stewardship scheme. *Journal of Applied Ecology*, *49*, 871–882. https://doi.org/10.1111/j.1365-2664.2012.02161.x

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, *29*, 1006–1016. https://doi.org/10.1111/cobi.12536

Benton, T. G., Bryant, D. M., Cole, L., & Crick, H. Q. P. (2002). Linking agricultural practice to insect and bird populations: A historical study over three decades. *Journal of Applied Ecology*, *39*, 673–687. https://doi.org/10.1046/j.1365-2664.2002.00745.x

Best, L. B., Campa, H. III, Kemp, K. E., Robel, R. J., Ryan, M. R., Savidge, J. A., ... Winterstein, S. R. (1998). Avian abundance in CRP and crop fields during winter in the Midwest. *The American Midland Naturalist*, *139*, 311–324. https://doi.org/10.1674/0003-0031(1998)139[0311:AAICAC]2.0.CO;2

Brennan, J. M., Bender, D. J., Contreras, T. A., & Fahrig, L. (2002). Focal patch landscape studies for wildlife management: Optimizing sampling effort across scales. In J. Liu, & W. W. Taylor (Eds.), *Integrating landscape ecology into natural resource management* (pp. 68–91). Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511613654

Brook, B. W., & Bradshaw, C. J. A. (2006). Strength of evidence for density denpendence in abundance time series of 1198 species. *Ecology*, *87*, 1445–1451. https://doi.org/10.1890/0012-9658(2006)87[1445:SOEFDD]2.0.CO;2

Buckingham, D., Evans, A., Morris, A., Orsman, C., & Yaxley, R. (1999). Use of set-aside land in winter by declining farmland bird species in the UK. *Bird Study*, *46*, 157–169. https://doi.org/10.1080/00063659909461127

Buckland, S. T. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. New York, NY: Oxford University Press.

Butler, S., Boccaccio, L., Gregory, R., Vorisek, P., & Norris, K. (2010). Quantifying the impact of land-use change to European farmland bird populations. *Agriculture, Ecosystems & Environment*, *137*, 348–357. https://doi.org/10.1016/j.agee.2010.03.005

Butler, S. J., Vickery, J. A., & Norris, K. (2007). Farmland biodiversity and the footprint of agriculture. *Science*, *315*, 381–384. https://doi.org/10.1126/science.1136607

Chandler, R. B., & Hepinstall-Cymerman, J. (2016). Estimating the spatial scales of landscape effects on abundance. *Landscape Ecology*, *31*, 1–12.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*, 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Concepción, E. D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., ... Verhulst, J. (2012). Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, *49*, 695–705.

Crosby, A. D., Elmore, R. D., Leslie, D. M. Jr., & Will, R. E. (2015). Looking beyond rare species as umbrella species: Northern Bobwhites (*Colinus virginianus*) and conservation of grassland and shrubland birds. *Biological Conservation*, *186*, 233–240. https://doi.org/10.1016/j.biocon.2015.03.018

Dail, D., & Madsen, L. (2011). Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics*, *67*, 577–587. https://doi.org/10.1111/j.1541-0420.2010.01465.x

del Monte-Luna, P., Brook, B. W., Zetina-Rejón, M. J., & Cruz-Escalona, V. H. (2004). The carrying capacity of ecosystems. *Global Ecology and Biogeography*, *13*, 485–495. https://doi.org/10.1111/j.1466-822X.2004.00131.x

Díaz, M., & Concepción, E. D. (2016). Enhancing the effectiveness of CAP greening as a conservation tool: A plea for regional targeting considering landscape constraints. *Current Landscape Ecology Reports*, *1*, 168–177. https://doi.org/10.1007/s40823-016-0017-6

Donald, P. F., & Evans, A. D. (2006). Habitat connectivity and matrix restoration: The wider implications of agri-environment schemes. *Journal of Applied Ecology*, *43*, 209–218. https://doi.org/10.1111/j.1365-2664.2006.01146.x

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*, 25–29. https://doi.org/10.1098/rspb.2000.1325

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, *65*, 169–175. https://doi.org/10.2307/3544901

Errington, P. L. (1945). Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena. *Ecological Monographs*, *15*, 2–34.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., … Martin, J. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, *14*, 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

Fischer, J., Brosi, B., Daily, G. C., Ehrlich, P. R., Goldman, R., Goldstein, J., … Tallis, H. (2008). Should agricultural policies encourage land sparing or wildlife-friendly farming? *Frontiers in Ecology and the Environment*, *6*, 380–385. https://doi.org/10.1890/070019

Guthery, F. S. (1997). A philosophy of habitat management for northern bobwhites. *Journal of Wildlife Management*, *61*, 291–301. https://doi.org/10.2307/3802584

Halloum, D. J., Leo, W., & Heard, L. (2000). *A comprehensive review of Farm Bill contributions to wildlife conservation, 1985–2000*. Madison, MS: USDA, NRCS, Wildlife Habitat Management Institute.

Hanski, I., & Gilpin, M. (1991). Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society*, *42*, 3–16. https://doi.org/10.1111/j.1095-8312.1991.tb00548.x

Hernández, F., Brennan, L. A., DeMaso, S. J., Sands, J. P., & Wester, D. B. (2013). On reversing the northern bobwhite population decline: 20 years later. *Wildlife Society Bulletin*, *37*, 177–188. https://doi.org/10.1002/wsb.223

Hostetler, J. A., & Chandler, R. B. (2015). Improved state-space models for inference about spatial and temporal variation in abundance from count data. *Ecology*, *96*, 1713–1723. https://doi.org/10.1890/14-1487.1

Jackson, H. B., & Fahrig, L. (2012). What size is a biologically relevant landscape? *Landscape Ecology*, *27*, 929–941. https://doi.org/10.1007/s10980-012-9757-9

Jackson, H. B., & Fahrig, L. (2015). Are ecologists conducting research at the optimal scale? *Global Ecology & Biogeography*, *24*, 52–63. https://doi.org/10.1111/geb.12233

Janke, A. K., & Gates, R. J. (2013). Home range and habitat selection of northern bobwhite coveys in an agricultural landscape. *Journal of Wildlife Management*, *77*, 405–413. https://doi.org/10.1002/jwmg.461

Johnson, D. H., & Schwartz, M. D. (1993). The conservation reserve program and grassland birds. *Conservation Biology*, *7*, 934–937. https://doi.org/10.1046/j.1523-1739.1993.740934.x

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. G., & Tscharntke, T. (2011). Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution*, *26*, 474–481. ISSN 0169-5347. https://doi.org/10.1016/j.tree.2011.05.009

Matthiopoulos, J., Fieberg, J., Aarts, G., Beyer, H. L., Morales, J. M., & Haydon, D. T. (2015). Establishing the link between habitat selection and animal population dynamics. *Ecological Monographs*, *85*, 413–436. https://doi.org/10.1890/14-2244.1

Merckx, T., Feber, R. E., Riordan, P., Townsend, M. C., Bourn, N. A., Parsons, M. S., & Macdonald, D. W. (2009). Optimizing the biodiversity gain from agri-environment schemes. *Agriculture, Ecosystems & Environment*, *130*, 177–182. https://doi.org/10.1016/j.agee.2009.01.006

Miguet, P., Jackson, H. B., Jackson, N. D., Martin, A. E., & Fahrig, L. (2016). What determines the spatial extent of landscape effects on species? *Landscape Ecology*, *31*, 1177–1194. https://doi.org/10.1007/s10980-015-0314-1

Morgan, J. J., Sprandel, G., Robinson, B. A., & Wethington, K. (2012). A county-based northern bobwhite habitat prioritization model for Kentucky. In C. E. Braun & T. V. Daily (Eds.), *Quail VII: Proceedings of the Seventh National Quail Symposium* (pp. 281–287). Knoxville, TN: The University of Tennessee, National Bobwhite Conservation Initiative.

Murphy, M. T., & Moore, F. (2003). Avian population trends within the evolving agricultural landscape of eastern and central United States. *Auk*, *120*, 20–34. https://doi.org/10.1642/0004-8038(2003)120[0020:APTWTE]2.0.CO;2

Nadeem, K., Moore, J. E., Zhang, Y., & Chipman, H. (2016). Integrating population dynamics models and distance sampling data: A spatial hierarchical state-space approach. *Ecology*, *97*, 1735–1745. https://doi.org/10.1890/15-1406.1

National Bobwhite Technical Committee. (2011). Mid-Atlantic regional issues in bobwhite conservation. In W. E. Palmer, T. M. Terhune & D. F. McKenzie (Eds.), *The national bobwhite conservation initiative: A range-wide plan for recovering bobwhites*. Knoxville, TN: National Bobwhite Technical Committee Technical Publication, Version 2.0.

Osborne, D. C., & Sparling, D. W. (2013). Multi-scale associations of grassland birds in response to cost-share management of conservation reserve program fields in Illinois. *Journal of Wildlife Management*, *77*, 920–930. https://doi.org/10.1002/jwmg.553

Pabian, S. E., Wilson, A. M., & Brittingham, M. C. (2013). Mixed responses of farmland birds to the Conservation Reserve Enhancement Program in Pennsylvania. *Journal of Wildlife Management*, *77*, 616–625. https://doi.org/10.1002/jwmg.514

Paloniemi, R., & Tikka, P. M. (2008). Ecological and social aspects of biodiversity conservation on private lands. *Environmental Science & Policy*, *11*, 336–346. https://doi.org/10.1016/j.envsci.2007.11.001

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling In K. Hornick, F. Leisch & A. Zeileis (Eds.), *Proceedings of the 3rd international workshop on distributed statistical computing* (pp. 1–10). Vienna, Austria.

Plummer, M. (2016). *rjags: Bayesian Graphical Models using MCMC*. R package version 4-6.

Pradel, R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, *52*, 703–709. https://doi.org/10.2307/2532908

Riffell, S. K., Monroe, A. P., Martin, J. A., Evans, K. O., Burger, L. W., & Smith, M. D. (2015). Response of non-grassland avian guilds to adjacent herbaceous field buffers: Testing the configuration of targeted conservation practices in agricultural landscapes. *Journal of Applied Ecology*, *52*, 300–309. https://doi.org/10.1111/1365-2664.12389

Riffell, S., Scognamillo, D., & Burger, L. W. (2008). Effects of the Conservation Reserve Program on northern bobwhite and grassland birds. *Environmental Monitoring and Assessment*, *146*, 309–323. https://doi.org/10.1007/s10661-007-0082-8

Roseberry, J. L., & Klimstra, W. D. (1984). *Population ecology of the bobwhite*. Carbondale, IL: Southern Illinois University Press.

Royle, J. A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, *60*, 108–115. https://doi.org/10.1111/j.0006-341X.2004.00142.x

Royle, J. A., Dawson, D. K., & Bates, S. (2004). Modeling abundance effects in distance sampling. *Ecology*, *85*, 1591–1597. https://doi.org/10.1890/03-3127

Smith, A. C., Fahrig, L., & Francis, C. M. (2011). Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography*, *34*, 103–113. https://doi.org/10.1111/j.1600-0587.2010.06201.x

Sollmann, R., Gardner, B., Chandler, R. B., Royle, J. A., & Sillett, T. S. (2015). An open-population hierarchical distance sampling model. *Ecology*, *96*, 325–331. https://doi.org/10.1890/14-1625.1

Sutherland, W. J. (1996). Predicting the consequences of habitat loss for migratory populations. *Proceedings: Biological Sciences*, *263*, 1325–1327.

Swift, T. L., & Hannon, S. J. (2010). Critical thresholds associated with habitat loss: A review of the concepts, evidence, and applications. *Biological Reviews*, *85*, 35–53. https://doi.org/10.1111/j.1469-185X.2009.00093.x

Taylor, W. P. (1934). Significance of extreme or intermittent conditions in distribution of species and management of natural resources, with a restatement of Liebig's law of minimum. *Ecology*, *15*, 374. https://doi.org/10.2307/1932352

Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., … Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, *151*, 53–59. https://doi.org/10.1016/j.biocon.2012.01.068

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., … Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes – Eight hypotheses. *Biological Reviews*, *87*, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Twedt, D. J., Wilson, R. R., & Keister, A. S. (2007). Spatial models of northern bobwhite populations for conservation planning. *Journal of Wildlife Management*, *71*, 1808–1818. https://doi.org/10.2193/2006-567

Veech, J. A. (2006). A comparison of landscapes occupied by increasing and decreasing populations of grassland birds. *Conservation Biology*, *20*, 1422–1432. https://doi.org/10.1111/j.1523-1739.2006.00487.x

Washburn, B. E., Barnes, T. G., & Sole, J. D. (2000). Improving northern bobwhite habitat by converting tall fescue fields to native warm-season grasses. *Wildlife Society Bulletin*, *28*, 97–104.

Whittingham, M. J. (2007). Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology*, *44*, 1–5.

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology*, *3*, 385–397. https://doi.org/10.2307/2389612

Yeiser, J. M., Baxley, D. L., Robinson, B. A., & Morgan, J. J. (2015). Using prescribed fire and herbicide to manage rank native warm season grass for northern bobwhite. *Journal of Wildlife Management*, *79*, 69–76. https://doi.org/10.1002/jwmg.813

Yeiser, J. M., Morgan, J. J., Baxley, D. L., Chandler, R. B., & Martin, J. A. (2018). Data from: Private land conservation has landscape-scale benefits for wildlife in agroecosystems. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.bn7p2f5

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Yeiser JM, Morgan JJ, Baxley DL, Chandler RB, Martin JA. Private land conservation has landscape-scale benefits for wildlife in agroecosystems. *J Appl Ecol*. 2018;55:1930–1939. https://doi.org/10.1111/1365-2664.13136