Articles

Correlates of Habitat Fragmentation and Northern Bobwhite Abundance in the Gulf Prairie Landscape Conservation Cooperative

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Abstract

The northern bobwhite *Colinus virginianus* has experienced range-wide declines over the past several decades, primarily due to habitat loss and habitat fragmentation. As northern bobwhite populations continue to decline, there is a need for studies that address the impact of habitat changes on population persistence at multiple spatial scales. Our goal was to assess changes in habitat and land use related to northern bobwhite declines across multiple spatial scales in Texas, Oklahoma, and Louisiana. We determined northern bobwhite trends for 1972–2012 using Breeding Bird Survey data. At the regional scale, we compared northern bobwhite population trends with road density (2000, 2012), human population (1970–2010), and land use (1974–2012). At the county and local scales, we compared class-level landscape metrics between counties with stable and declining northern bobwhite abundances using Student’s t-tests. Northern bobwhite populations decreased from 45.95 ± 1.01 birds/route in 1970 to 11.55 ± 0.64 birds/route in 2012. Road density and human population increased by 3,331.32 ± 66.28 m/km² and 42,873 ± 8,687 people/county, respectively. Percent pasture and rangeland was relatively stable, as was percent woodland. Alternatively, the percentage of other land (houses, roads, wasteland) increased. At the county scale, Texas and Oklahoma counties with declining northern bobwhite populations had higher road densities, larger patches of pasture, smaller patches of woodland, and larger patches of cropland compared with stable populations. At the local scale, Texas and Oklahoma counties with declining northern bobwhite populations had less woody cover in smaller patches, and fewer but larger patches of herbaceous and bare ground, compared with populations with stable abundance. Therefore, managers can provide woody cover and reduce cropland effects at the local scale to support stable quail populations; however, the large-scale drivers of northern bobwhite decline, which are human population growth and resulting habitat loss, will be an important aspect of northern bobwhite conservation and management in the future.

Keywords: Breeding Bird Survey; *Colinus virginianus*; habitat fragmentation; land use; northern bobwhite; urban growth.

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**Introduction**

The northern bobwhite *Colinus virginianus* has experienced range-wide declines over the past several decades (Brennan 1991; Brennan and Kuvlesky 2005). Although many factors have contributed to these declines across the landscape (Guthery 2000; Burger 2002), the primary factor is reduction of habitat through loss and fragmentation (Peterson et al. 2002; Brennan and Kuvlesky 2005; Veech 2006; Hernández et al. 2012). Factors of habitat fragmentation include conversion of small farms with sufficient edge cover into large-scale clean farming (Brennan 1991; Peterson et al. 2002; Twedt et al. 2007), altered forest management (Brennan 1991), and increasing urbanization (Brennan and Kuvlesky 2005). Habitat fragmentation results in smaller patches from more contiguous larger patches (Bender et al. 1998), with potentially reduced nesting success and increased rates of predation and parasitism (Johnson and Temple 1990; Vickery et al. 1992; Burger et al. 1994; Winter et al. 2000; Herkert et al. 2003). Moreover, fragmentation processes can result in higher probabilities of local extinction with lower probabilities of recolonization, particularly for grassland bird species where habitat spatial structure is an important variable to occupancy (Herkert 1994; Vickery et al. 1994; Walk and Warner 1999; Winter and Faaborg 1999).

When assessing the potential causes of population decline, an understanding of the relevant spatial scale is critical. For example, local-scale analyses may reveal effects of vegetation structure on nest site selection (Pribil and Picman 1997), occupancy (Wiens et al. 1987), or abundance (Thompson et al. 2002) for avian species. Alternatively, broad-scale analyses may reveal patterns of habitat fragmentation and community structure associated with avian productivity (Thompson et al. 2002) and abundance (Hagan et al. 1997). Cross-scale dependency further complicates the issue. Effects of vegetation structure or abundance of predators at local spatial scales may be dependent upon the effect of the landscape, particularly in fragmented habitats (Chalfoun et al. 2002; Thompson et al. 2002).

Recent studies have focused on large-scale factors that may be affecting declines in grassland birds (Peterson et al. 2002; Murphy 2003; Veech 2006; Rho et al. 2015). For northern bobwhites, restoration that is limited to small patches is related to low probability of colonization and high individual mortality (Fies et al. 2002; Terhune et al. 2010). Therefore, large-scale factors are important to managing the species. Sands et al. (2012) evaluated northern bobwhite habitat requirements for population persistence at different harvest rates (0–40%). They found that northern bobwhite populations may require 8–96 km² of habitat for 95% probability of metapopulation persistence, considerably more area than previously considered important given the individual small home ranges reported for this species (0.01–0.58 km², Miller et al. 2017). However, few studies have addressed the multiple scales at which ecological, demographic, or agricultural processes may be affecting northern bobwhite population declines.

With the continuing decline of northern bobwhite populations and the findings from Sands et al. (2012), there has been an interest in managing northern bobwhite habitat at a larger scale. Studies that approached both local and larger spatial scales include Seckinger et al. (2008) and Potter et al. (2011). At the landscape level, both Peterson et al. (2002) and Veech (2006) compared changes in land use with northern bobwhite population trends. Although Peterson et al. (2002) did not find causes for the decline that could be applied across the range, Veech (2006) found that declining populations of northern bobwhite were associated with less cropland and pastureland, and more woodland and barren land. This creates some confusion for how to best manage northern bobwhite populations. Scale may be an important factor in interpreting these results. The use of matching scales between spatial databases and the ecological scales of the observed processes is critical to address management priorities and conservation strategies (Perotto-Baldivieso et al. 2009). The use of different spatial scales to address one ecological scale will have an impact on the interpretation of the results. More importantly, it is now becoming increasingly important to address wildlife-habitat modeling using more than one scale (Perotto-Baldivieso et al. 2011; McGarigal et al. 2016). Therefore, incorporating multiple scales into planning landscape conservation frameworks can contribute to the prioritization of strategies for restoration and conservation of cover types (Didham et al. 2012; Rappaport et al. 2015). Determining the domains of scale may be an important step in building a framework to assess habitat for a species (Wheatley 2010), and empirical assessments...
using this framework may be useful to measure the processes affecting northern bobwhite populations at different domains of scale. Domains of scale are defined as areas with no significant change along the scale continuum (Wiens 1989; Wheatley 2010). These areas of no change could be related to levels to organization (e.g., populations). Thus, it may be possible to use different extents within the same domain to quantify landscape-level habitat characteristics. We lack empirical quantified analyses that address habitat changes and their impact on northern bobwhite population trends and persistence at multiple spatial scales.

Our goal was to assess changes in habitat and land use and their relationship to northern bobwhite declines at multiple spatial scales. Our first objective was to compare northern bobwhite declines over the past four decades to changes in land use across three states, Texas, Oklahoma, and Louisiana. Our second objective was to compare counties with declining and stable northern bobwhite populations and their differences in land cover types. We expected that at on a landscape scale, higher rates of clean farming and urbanization would occur in areas where northern bobwhite populations have declined. Our third objective was to compare local differences in areas with stable and declining northern bobwhite populations. We expected that spatial structure of the vegetation, particularly woodland, would reveal specific patterns for northern bobwhite habitat.

Methods

Vegetation included blackjack Quercus marilandica, post Q. stellata, and white oak Q. alba in Oklahoma; oaks, honey mesquite Prosopis glandulosa, and huisache Vachellia farnesiana farnesiana in Texas; and loblolly Pinus taeda and longleaf pine P. palustris in Louisiana (Woods et al. 2005; Daigle et al. 2006; Hernández et al. 2007; Texas Parks and Wildlife 2016). In Louisiana’s Southeastern Plains, bald cypress Taxodium distichum and tupelo Nyssa spp. were also common (Daigle et al. 2006). Grasses included little bluestem Schizachyrium scoparium, indiangrass Sorghastrum nutans, buffalo grass Bouteloua dactyloides, and bufflegrass Pennisetum ciliare (Woods et al. 2005; Daigle et al. 2006; Hernández et al. 2007). Coastal prairies were dominated by gulf Spartina spartinae and smooth cordgrass S. alterniflora (Daigle et al. 2006; Hernández et al. 2007). Average annual precipitation varied from <30 cm in the Trans Pecos of Texas (Texas Parks and Wildlife 2016; Larkin and Bomar 1983) to 157 cm in eastern Louisiana. Elevation varied from sea level on the Gulf Coast to 2,667 m (Guadalupe Peak) in the Trans Pecos of Texas, 1,739 m (Black Mesa) in the Southwestern Tablelands of Oklahoma, and 163 m (Driskill Mountains) in the South Central Plains of Louisiana (m above sea level).

We assessed northern bobwhite population trends in Texas, Oklahoma, and Louisiana, and then assessed the influence of habitat loss and fragmentation on these trends using a hierarchical approach with three spatial scales: regional, county, and local (Table 1). We used a multilevel, multiscale approach (McGarigal et al. 2016). The regional level focused on northern bobwhite population trends and land use across four decades. For this step we sampled the extent of Texas, Oklahoma, and Louisiana at a grain of 4 km². We then used the analysis of northern bobwhite population trends to compare current vegetation types in randomly selected stable and declining populations (6/state). At the county level, we used three extents, 8, 50, and 96 km², at a grain of 900 m², based on the findings by Sands et al. (2012) for 95% metapopulation persistence. Rather than selecting only one extent, we decided to use the values reported by Sands et al. (2012) and evaluate whether three extents within the same domain of scale would yield similar results, therefore providing empirical evidence for domains of scales as a level of organization for northern bobwhites. The county scale generated information for wildlife biologists attempting to assess areas relevant to metapopulations, and information for stakeholders and decision-makers attempting to delineate strategies and local policies for wildlife habitat planning, restoration, and conservation. We conducted the third analysis at the local level to assess the spatial structure of vegetation that is important to northern bobwhite ranch and farm management. We used the mean northern bobwhite home range from Miller et al. (2017; 0.15 km²) for extent, with a grain of 1 m². This provided information useful to local ranchers and landowners managing landscapes for maintenance or improvement of northern bobwhite habitat.

Northern bobwhite population trends

We determined northern bobwhite population trends using the North American Breeding Bird Survey data (https://www.pwrc.usgs.gov/bbs/). The Breeding Bird Survey is a citizen science project consisting of >4000 random routes across North America and Canada. Counters navigate a 25.5-mi (41-km) route and stop every 0.5 mi (0.8 km) to conduct a 3-min point count. Using the starting point of each route, from 1970 to 2014, we interpolated route totals using kriging and inverse distance weighting in ArcGIS v. 10.3.1 (Peterson et al. 2002; Okay 2004; Rho et al. 2015). We set the resulting abundance maps to a resolution of 4 km². Northern bobwhite populations exhibit a boom and bust pattern (Peterson 2001; Hernández and Peterson 2007; Lusk et al. 2007); therefore, we also accounted for annual variability from 1972 to 2012 by calculating 5-y rolling averages. For example, we calculated the average of 1972 as 1970–1974 (Peterson et al. 2002; Rho et al. 2015). We summarized the mean number of northern bobwhite/route for each county and then calculated the mean for each year across the region. We calculated the statistical range as the difference between the largest and smallest northern bobwhite counts for each county. This represents the variability across the counts for each year and provides information about the local abundance within the landscape. We assessed trends in northern bobwhite mean and range across the region between 1970 and 2012 using a linear regression model.
### Regional level analysis

We compared road density, human population, and land use with northern bobwhite populations across Texas, Oklahoma, and Louisiana. We quantified these effects at three different temporal scales, based on available data (Table 1). We obtained road density (2000, 2012) and human population (1970, 1980, 1990, 2000, and 2010) data from the United States Census Bureau (http://www.census.gov/en.html), and land use data from the Census of Agriculture (http://www.agcensus.usda.gov/) for 1974, 1978, 1987, 1997, 2002, and 2012. Data for the period 1978–1997 were derived from Okay (2004). We calculated road density as meters of road/km² and then changed the resolution by summing the density for 4 1-km² pixels into 4-km² pixels to match the northern bobwhite abundance spatial resolution. We used the centroid of the county with county-level census data to interpolate the number of humans/km².

Land use was classified into total pasture and rangeland, total woodland, total cropland, and total other land. Pasture and rangeland included pasture and grazed cropland, pastured woodland, and other rangeland. Cropland included harvested, pasture and grazed, cover and legumes, failed, summer and fallow, and idle cropland. Other land included pasture and range not included in cropland or woodland, houses, ponds, roads, and wasteland. We also determined amount of cropland placed in the Conservation Reserve Program (CRP), and created buffers at 8, 50, and 96 km² for each point. We obtained 2013 Landsat 8 Imagery from GLOVIS (http://glovis.usgs.gov/) and we reclassified images following the U.S. Census of Agriculture categories to 6 classes: pasture and rangeland, woodland, cropland, other land (infrastructure, barren, wasteland, etc.), water, and roads (ERDAS IMAGINE 2015, Hexagon). We used buffered areas to clip the classified images and then we quantified road density (m/km²). We then determined the following class-level landscape metrics: percentage of the landscape (%), mean patch area (km²), largest patch index (%), patch density (# patches/km²), edge density (m/ km²), and Euclidean nearest neighbor (m; Perotto-Baldiveso et al. 2011; Young et al. 2014), using Fragstats.

### County level analysis

At this scale we compared vegetation from 2013 in three habitat sizes required for 95% metapopulation persistence at 0–40% harvest (8, 50, 96 km²; Sands et al. 2012). First, we excluded those parishes and counties where northern bobwhite abundance indices have consistently been low or nonexistent within the timeframe of the Breeding Bird Survey using a breakpoint of 30 birds/route. In 1972 and 1983, Breeding Bird Survey estimates indicated exceptionally high northern bobwhite abundances. For each of those years we determined the minimum number of birds/route for those routes above the 25% quartile (40–50 birds/route). A breakpoint at 40 birds excluded all parishes in Louisiana, so we reduced the breakpoint to 30 birds/route (76.31% of 363 counties/parishes in 1972 and 60.94% of 361 counties/parishes in 1983). This process excluded 115 counties and parishes, leaving 280 counties and parishes with stable and declining northern bobwhite populations (Texas, n = 184; Oklahoma, n = 71; Louisiana, n = 25). From this subsample, we randomly selected three counties in Oklahoma (Grady, Love, and Osage), three counties in Texas (Erath, Fisher, and Jim Hogg), and six parishes in Louisiana (Calcasieu, Franklin, Jackson, St. Tammany, Union, and Vernon). These parishes or counties represented northern bobwhite populations that have declined significantly since the 1970s. For counties where northern bobwhite populations have remained relatively stable (i.e., numbers were similar) between 1970 and 2012, we randomly selected three counties in Oklahoma (Grant, Pushmataha, and Roger Mills) and three counties in Texas (Donley, Frio, and Refugio). In Louisiana, northern bobwhite populations have declined across the state; therefore, we did not sample any parishes with stable populations.

We established 10 random points/county or parish (Declining: Texas, n = 30, Oklahoma n = 30, and Louisiana, n = 60; Stable: Texas, n = 30; Oklahoma n = 30; total number of sample points n = 180), and created buffers at 8, 50, and 96 km² for each point. We obtained 2013 Landsat 8 Imagery from GLOVIS (http://glovis.usgs.gov/) and we reclassified images following the U.S. Census of Agriculture categories to 6 classes: pasture and rangeland, woodland, cropland, other land (infrastructure, barren, wasteland, etc.), water, and roads (ERDAS IMAGINE 2015, Hexagon). We used buffered areas to clip the classified images and then we quantified road density (m/km²). We then determined the following class-level landscape metrics: percentage of the landscape (%), mean patch area (km²), largest patch index (%), patch density (# patches/km²), edge density (m/ km²), and Euclidean nearest neighbor (m; Perotto-Baldiveso et al. 2011; Young et al. 2014), using Fragstats.

### Table 1. Spatial and temporal scale (extent and resolution) used for hierarchical analyses on changing land use and northern bobwhite *Colinus virginianus* abundance trends. We used data from the North American Breeding Bird Survey (BBS), United States (U.S.) Census, Landsat Imagery, and National Agriculture Imagery Program (NAIP).

| Analysis                  | Data source                  | Extent            | Resolution | Temporal scale | Resolution |
|---------------------------|------------------------------|-------------------|------------|----------------|------------|
| Northern bobwhite abundance | BBS                          | 1,012,918 km² *   | 4 km²      | 1970–2014      | Annual     |
|                           |                              |                   |            | 5-yr averages: 1972–2012 |
| Regional                  | U.S. Census                  | 1,012,918 km²     | 4 km²      | 2000–2012      | 2000, 2012 |
|                           |                              |                   |            | 1970–2010      | 1970, 1980, 1990, 2000, 2010 |
| Road density              |                              | —                 | —          | —              | —          |
| Human population          |                              | —                 | —          | —              | —          |
| Regional                  | U.S. Census of Agriculture   | 1,012,918 km²     | 4 km²      | 1974–2012      | 1974, 1978, 1987, 1997, 2002, 2007, 2012 |
| County                    | Landsat 8 Imagery            | 900 m²            |            | 2013           | 2013       |
| Local                     | NAIP                         | County            | 1 m²       | 2014           | 2014       |

* Refers to the area of Texas, Oklahoma, and Louisiana combined.
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v. 4.2.1 (McGarigal et al. 2012). We compared road density and landscape metrics between declining and stable populations in Texas and Oklahoma using Student’s t-tests ($\alpha = 0.05$). Data passed tests for normality for these 12 counties.

Local level analyses

We focused this analysis within the same populations from the county level analysis. We generated three random points per county (Texas and Oklahoma) or parish (Louisiana) using the Create Random Points tool in ArcGIS, in order to select three random areas on a 7.5-min topographic map. Within each of these three areas we randomly selected one National Agriculture Imagery Program 1-m resolution digital orthophoto quarter quads from 2014. For each quad, we classified vegetation spatial structure into four classes: woody, herbaceous, bare ground, and water. Images were assessed for accuracy using similar methods to Pulighe et al. (2016). Within each of the three quads we generated random points ($n = 25$/quad). This resulted in 75 points/county. For each point we created a 0.15-km$^2$ buffer to represent home range. We acknowledge the variation in reported home ranges for the area, from 0.01 km$^2$ in Jim Hogg County (Taylor and Guthery 1994) to 0.58 km$^2$ in southeastern Louisiana (see Bell et al. in Lee 1994). We chose 0.15 km$^2$ to represent home range from Haines et al. (2004) and Miller et al. (2017). For each buffered area, we quantified vegetation spatial structure using the following landscape metrics in FRAGSTATS v. 4.2.1: percentage of the landscape (%), mean patch area (km$^2$), largest patch index (%), patch density (# patches/km$^2$), edge density (m/km$^2$), and Euclidean nearest neighbor (m; Perotto-Baldivieso et al. 2011; Young et al. 2014). We compared landscape metrics between declining and stable northern bobwhite populations in Texas and Oklahoma using Student’s t-tests ($\alpha = 0.05$). Results are given as ± standard error (SE) except where noted otherwise. Louisiana parishes were not included in statistical analyses because of the lack of parishes with stable northern bobwhite populations for comparison. However, descriptive statistics for these parishes are included as supplemental material.

Results

Northern bobwhite population trends

We found that northern bobwhite populations in Texas, Oklahoma, and Louisiana have declined significantly (Figure 1), from 45.95 ± 1.01 birds/route in 1970 to 11.55 ± 0.64 birds/route in 2012 ($R^2 = 0.95, P < 0.001$; $y_0 = 1929.21 [SE = 67.91]; a = 0.95 [SE = 0.03]$). The range in northern bobwhite abundance decreased from 18.29 ± 0.97 birds/count in 1970 to 8.98 ± 0.49 birds/count in 2012 (Figure 1). The overall trends between 1970 and 2012 show that northern bobwhite populations with declining abundances occurred in a pattern from South Texas (Laredo) northeast to northeast Oklahoma (Tulsa; Figure S1, Supplemental Material). A smaller yet similar pattern occurred in Louisiana (Leesville and Alexandria, northeast to Monroe; Figure S1, Supplemental Material).

Regional level

Road density increased from 2000 to 2012 and human population increased from 1970 to 2010. Road density increased from averages of 7,063.01 ± 157.96 m/4 km$^2$ in 2000 to 10,394.33 ± 244.84 m/4 km$^2$ in 2012, while northern bobwhite abundances decreased from averages of 18.03 ± 0.89 birds/route in 2000 to 11.55 ± 0.64 birds/route in 2012 (Figure 2a). Human populations increased from averages of 45,727 ± 7,516 people/county in 1970 to 88,600 ± 16,203 people/county in 2010. Comparatively, northern bobwhite abundance declined from averages of 45.93 ± 1.01 birds/route in 1970 to 11.93 ± 0.66 birds/route in 2010 (Figure 2b).

Total pastureland increased (Figure S2, Supplemental Material) from 34% in 1974 to 48% in 2012, total woodland remained at 5–6% (Figure S2, Supplemental Material), and percent cropland was similar between 1974 and 2002 (~26%) but decreased to 19% in 2012 (Figure S2, Supplemental Material). Northern bobwhite abundance trends decreased across all land-use cover types at the regional scale (Figure 3). Other land (infrastructure, barren, wasteland) increased from 40% in 1974 to 46% in 2012. The total percentage of CRP land increased to 2% by 2012 from 1987. The increase in percent pastureland appeared to be related to changes in northern bobwhite populations, while percent woodland and cropland were not related to these changes (Figure 3).

County level

For populations in Texas and Oklahoma, road density was higher for populations with declining abundance at all three extents, compared with populations with stable abundance (Table 2; Table S1, Supplemental Material). At the 50-km$^2$ metapopulation level, this difference was significant ($t_{111} = 2.02, P = 0.046$; Table S1, Supplemental Material). This supports the findings of the region-wide analysis: road density as a qualitative measure for urbanization correlates with northern bobwhite populations that are in decline. We did not include Louisiana populations in statistical analyses, but the mean and standard error for class-level landscape characteristics are shown in Table S2 (Supplemental Material).

Pasture and rangeland cover. In Texas and Oklahoma, populations with declining abundance had higher mean patch areas across the three extents (significant at 50 km$^2$: $t_{66} = 2.12, P = 0.038$, and 96 km$^2$: $t_{79} = 2.04, P = 0.044$), compared with populations with stable abundance (Table 2; Table S1, Supplemental Material). These declining populations also had higher edge densities of pasture and rangeland (significant at 96 km$^2$: $t_{115} = 2.05, P = 0.043$). While populations with declining abundance had higher mean patch areas, the Euclidean nearest neighbor distance between patches was lower across all
Northern bobwhite *Colinus virginianus* declines in abundance from 1970 to 2012 across Texas, Oklahoma, and Louisiana. Data are from the North American Breeding Bird Survey. Maps (a) depict northern bobwhite abundance for 1970 and 2010. Linear regressions (b) for the mean and range (highest count–lowest count) are represented with a black line. The black dot represents the mean or range of the northern bobwhite counts, and the blue and red lines represent the 95% confidence band and 95% prediction band, respectively. Beginning in 1972, the 5-y rolling average of northern bobwhite/route is shown.

Figure 1. Northern bobwhite *Colinus virginianus* declines in abundance from 1970 to 2012 across Texas, Oklahoma, and Louisiana. Data are from the North American Breeding Bird Survey. Maps (a) depict northern bobwhite abundance for 1970 and 2010. Linear regressions (b) for the mean and range (highest count–lowest count) are represented with a black line. The black dot represents the mean or range of the northern bobwhite counts, and the blue and red lines represent the 95% confidence band and 95% prediction band, respectively. Beginning in 1972, the 5-y rolling average of northern bobwhite/route is shown.
extents, compared with populations with stable abundance (significant at 50 km$^2$: $t_{66} = -2.85$, $P = 0.005$, and 96 km$^2$: $t_{79} = -3.40$, $P = 0.001$; Table 2; Table S1, Supplemental Material).

Woodland cover. Across all three extents, populations with declining abundance had smaller patches and largest patch indices compared with populations with stable abundance (Table 2; Table S1, Supplemental Material). Mean patch area was significantly smaller at 96 km$^2$ ($t_{62} = -2.02$, $P = 0.048$; Table 2) and largest patch indices were significantly smaller at 50 km$^2$ ($t_{58} = -2.00$, $P = 0.048$) and 96 km$^2$ ($t_{62} = -2.40$, $P = 0.019$; Table 2; Table S1, Supplemental Material). These patches were more numerous in declining populations across all three metapopulation levels (8 km$^2$: $t_{77} = 3.32$, $P = 0.001$; 50 km$^2$: $t_{71} = 3.87$, $P < 0.001$; 96 km$^2$: $t_{70} = 3.98$, $P < 0.001$; Table 2; Table S1, Supplemental Material).

Cropland cover. For populations with declining abundance in Texas and Oklahoma, percent land cover and largest patch indices were larger than in stable populations at all three extents. In the case of largest patch indices, the difference was significant at 8 km$^2$ ($t_{34} = 2.05$, $P = 0.043$; Table S1, Supplemental Material). In these populations with declining northern bobwhite abundance, mean patch area was larger while patch density and edge density were lower, but the difference was not statistically significant.

**Figure 2.** Effects of road density from 2000 and 2014 (a) and human population growth from 1970 to 2010 (b) on northern bobwhite *Colinus virginianus* abundance (birds/route) in Texas, Oklahoma, and Louisiana. Beginning in 1972, the 5-y rolling average of northern bobwhite/route is shown.

**Figure 3.** Changes in percent of the landscape (% land, U.S. Census of Agriculture) in pasture and rangeland, woodland, and cropland compared with changes on northern bobwhite *Colinus virginianus* abundance (birds/route) in Texas, Oklahoma, and Louisiana. Northern bobwhite/route represents 5-y averages from the North American Breeding Bird Survey for 1974, 1978, 1987, 1997, 2002, 2007, and 2012. Land use data from 1978 to 1997 were obtained from Okay 2004. Beginning in 1972, the 5-y rolling average of northern bobwhite/route is shown.

**Local level**

**Woody cover.** Declining populations in Texas and Oklahoma were associated with significantly lower percentages of woody cover ($t_{729} = -4.73$, $P < 0.001$), mean patch areas ($t_{450} = -2.87$, $P = 0.004$), and largest patch indices ($t_{720} = -3.38$, $P < 0.001$; Table 3, Figure 4). Patch density and edge density were also significantly lower in declining northern bobwhite populations ($t_{719} = -5.96$, $P < 0.001$, $t_{797} = -5.34$, $P < 0.001$, respectively). Populations with stable abundance had ~20% woody cover with more patches, more edge, and higher connectivity than populations with declining abundance (Figure 4).

**Herbaceous and bare ground.** Populations with declining abundance in Texas and Oklahoma had significantly more herbaceous cover and bare ground ($t_{1,729} = 2.08$, $P = 0.037$), with higher largest patch indices ($t_{1,792} = 2.01$, $P = 0.044$, Table 3). Patch density and edge density were significantly lower ($t_{1,545} = -5.80$, $P < 0.001$, $t_{1,611} = 6.94$, $P < 0.001$, respectively). Therefore, these populations were associated with fewer patches of herbaceous cover and bare ground and less edge than populations with stable abundance (Table 3, Figure 4). Similar to the county level, we did not include declining populations in Louisiana in statistical analyses; however, the mean and standard error are shown in Table S3 (Supplemental Material).

**Discussion**

Our studies found that effects of human population growth and infrastructure development were evident on a regional scale, while effects of pasture, woodland, and crop cover were more evident at the county and local scales. Spatial scale is an important consideration in
species abundance analyses. Local scale effects, such as community structure edge and patch effects, may be constrained by the effects of the landscape (McGarigal and McComb 1995). Alternatively, changes in landscape may have a stronger effect on abundance for particular species (Thompson et al. 2002; Stephens et al. 2003).

**Regional patterns**

Our findings at the regional scale not only coincide with national and global trends reported for human population growth and the subsequent negative impacts on biodiversity but also provide a quantitative approach that highlights the impact of human activities on an umbrella species such as the northern bobwhite. Human

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**Table 2.** Comparison of road density and 2013 class-level landscape metrics in counties with declining and stable northern bobwhite Colinus virginianus abundance. Counties with declining abundance included Erath, Fisher, and Jim Hogg in Texas, and Grady, Love, and Osage in Oklahoma (TX/OK –). Counties with stable abundance included Donley, Frio, and Refugio in Texas, and Grant, Pushmataha, and Roger Mills in Oklahoma (TX/OK +). Ten random points/county were sampled at three buffer sizes that represented 95% metapopulation persistence, for simplicity only the largest buffer (96 km²) is shown. Statistics in bold are significant (α = 0.05).

*Table 2.** Continued.

| Metric                          | TX/OK – | TX/OK + |
|--------------------------------|---------|---------|
| **Road density (m/km²)**       |         |         |
| Mean                           | 2,319.18| 2,008.84|
| SE                             | 130.65  | 101.77  |
| Statistic                      |          |         |
| —                              | $t_{111} = 1.87$ | 
| $P = 0.064$                    |         |         |
| **Pasture and rangeland**      |         |         |
| Percent of the landscape (%)   |         |         |
| Mean                           | 42.91   | 39.04   |
| SE                             | 2.60    | 2.17    |
| Statistic                      |          |         |
| —                              | $t_{114} = 1.14$ | 
| $P = 0.255$                    |         |         |
| Mean patch area (km²)          |         |         |
| Mean                           | 0.15    | 0.07    |
| SE                             | 0.03    | 0.01    |
| Statistic                      |          |         |
| —                              | $t_{29} = 2.04$ | 
| $P = 0.044$                    |         |         |
| Largest patch index (%)        |         |         |
| Mean                           | 28.17   | 25.21   |
| SE                             | 3.60    | 2.81    |
| Statistic                      |          |         |
| —                              | $t_{111} = 0.65$ | 
| $P = 0.519$                    |         |         |
| **Patch density (#/km²)**      |         |         |
| Mean                           | 11.46   | 9.85    |
| SE                             | 0.96    | 0.67    |
| Statistic                      |          |         |
| —                              | $t_{103} = 1.34$ | 
| $P = 0.183$                    |         |         |
| Edge density (m/km²)           |         |         |
| Mean                           | 14,390.48| 12,832.50|
| SE                             | 495.30  | 576.28  |
| Statistic                      |          |         |
| —                              | $t_{115} = 2.05$ | 
| $P = 0.043$                    |         |         |
| Euclidean nearest neighbor (m) |         |         |
| Mean                           | 70.36   | 74.79   |
| SE                             | 0.67    | 1.12    |
| Statistic                      |          |         |
| —                              | $t_{56} = 3.40$ | 
| $P = 0.001$                    |         |         |
| **Woodland**                   |         |         |
| Percent of the landscape (%)   |         |         |
| Mean                           | 18.48   | 24.00   |
| SE                             | 1.78    | 2.76    |
| Statistic                      |          |         |
| —                              | $t_{101} = -1.68$ | 
| $P = 0.095$                    |         |         |
| Mean patch area (km²)          |         |         |
| Mean                           | 0.02    | 0.06    |
| SE                             | 0.003   | 0.02    |
| Statistic                      |          |         |
| —                              | $t_{32} = -2.02$ | 
| $P = 0.048$                    |         |         |
| Largest patch index (%)        |         |         |
| Mean                           | 4.88    | 11.79   |
| SE                             | 1.17    | 2.63    |
| Statistic                      |          |         |
| —                              | $t_{32} = -2.40$ | 
| $P = 0.019$                    |         |         |
The decrease in northern bobwhite populations can be explained by a combination of factors, including the development of urban areas, the loss of small cropland with edge, the use of herbicides, and improved pastures. The decrease in variability of northern bobwhite abundance (i.e., decreased range) across the landscape may also increase vulnerability for the species. Northern bobwhite populations experience a boom and bust pattern, and a high variability in abundance may provide a source of migrants into a population experiencing a threat of extinction.

We found that percent pasture and rangeland increased from 1974 to 2012. In Texas, this pasture and range cover included honey mesquite and eastern red cedar Juniperus virginiana, which encroached on prairie from overgrazing, windbreaks, and fire suppression (Brennan and Kuvlesky 2005). However, while percent of pasture cover may not have changed drastically over the past 40 y, the composition of that pasture has. Approximately 10,000 km² of rangeland in Oklahoma and Texas have been converted to old world bluestem (McCoy et al. 1992; White and Dewald 1996). Agricultural, commercial, and urban developments have reduced coastal prairies to 1% of the 34,000 km² originally in Texas and Louisiana (Smeins et al. 1991). Although efforts to restore habitat are underway (Oaks and Prairies Joint Venture), much of the area is now composed of nonnative cool-season grass species. These species, particularly when they form monotypic stands, may not be suitable habitat for northern bobwhite, lacking adequate vegetation composition and structure (Guthery 2000; Collins et al. 2009; Janke and Gates 2013). Northern bobwhite populations require perennial forbs, seeds, and insects (Guthery 2000; Collins et al. 2009), and nesting, foraging, and brood rearing are improved when warm season grasses are present (Burger et al. 1990; Guthery 2000).

The Census of Agriculture combines pasture and rangeland into one category. This includes meadow, prairie, and range, with bunchgrass, shortgrass, buffalo

### Table 3. Comparison of 2014 class-level landscape metrics in counties with declining and stable northern bobwhite Colinus virginianus abundance. Counties with declining abundance included Erath, Fisher, and Jim Hogg in Texas, and Grady, Love, and Osage in Oklahoma (TX/OK —). Counties with stable abundance included Donley, Frio, and Refugio in Texas, and Grant, Pushmataha, and Roger Mills in Oklahoma (TX/OK +). Twenty-five random points per county were sampled at 0.15 km², representing northern bobwhite home range. Statistics in bold are significant (α = 0.05).

| Woody cover                                      | TX/OK —  | TX/OK +  |
|-------------------------------------------------|----------|----------|
| Percent of the landscape (%)                    | Mean     | 14.62    | 20.97    |
| Standard error                                  | 0.74     | 1.12     |
| Statistic                                        | $t_{779} = -4.73$ | $P < 0.001$ |
| Mean patch area (km$^2$)                         | Mean     | 0.00006  | 0.0005   |
| Standard error                                  | 0.000005 | 0.0001   |
| Statistic                                        | $t_{450} = -2.87$ | $P = 0.004$ |
| Largest patch index (%)                         | Mean     | 7.04     | 11.02    |
| Standard error                                  | 0.59     | 1.02     |
| Statistic                                        | $t_{728} = -3.38$ | $P < 0.001$ |
| Patch density (#/km$^2$)                         | Mean     | 3,576.90 | 5,364.65 |
| Standard error                                  | 150.07   | 150.07   |
| Statistic                                        | $t_{719} = -5.96$ | $P < 0.001$ |
| Edge density (m/km$^2$)                          | Mean     | 113,791.00 | 158,081.00 |
| Standard error                                  | 4,702.61 | 6,828.73 |
| Statistic                                        | $t_{799} = -5.34$ | $P < 0.001$ |
| Euclidean nearest neighbor (m)                   | Mean     | 6.06     | 4.67     |
| Standard error                                  | 0.65     | 0.34     |
| Statistic                                        | $t_{9} = 1.90$ | $P = 0.057$ |

### Table 3. Continued.

| Herbaceous cover and bare ground                | TX/OK —  | TX/OK +  |
|-------------------------------------------------|----------|----------|
| Percent of the landscape (%)                    | Mean     | 42.16    | 38.77    |
| Standard error                                  | 1.18     | 1.11     |
| Statistic                                        | $t_{729} = 2.08$ | $P = 0.037$ |
| Mean patch area (km$^2$)                         | Mean     | 0.003    | 0.003    |
| Standard error                                  | 0.0005   | 0.0006   |
| Statistic                                        | $t_{692} = -0.48$ | $P = 0.629$ |
| Largest patch index (%)                         | Mean     | 35.16    | 31.84    |
| Standard error                                  | 1.20     | 1.13     |
| Statistic                                        | $t_{729} = 2.01$ | $P = 0.044$ |
| Patch density (#/km$^2$)                         | Mean     | 3,249.85 | 4,561.17 |
| Standard error                                  | 123.28   | 189.46   |
| Statistic                                        | $t_{545} = -5.80$ | $P < 0.001$ |
Figure 4. Class-level landscape metrics for 2014 at the 0.15-km² buffer for home range for declining and stable northern bobwhite *Colinus virginianus* populations in Texas and Oklahoma. Declining populations sampled included Erath, Fisher, and Jim Hogg in Texas, and Grady, Love, and Osage in Oklahoma. Stable populations sampled included Donley, Frio, and Refugio in Texas, and Grant, Pushmataha, and Roger Mills in Oklahoma. Asterisks (*) denote significant differences in the means for landscape metrics between declining and stable populations in Texas and Oklahoma ($\alpha = 0.05$). Declining northern bobwhite populations were associated with smaller patches of woodland and larger patches of herbaceous vegetation with bare ground.
Northern bobwhite populations likely benefitted from the settlers who cleared small areas for agriculture, creating an array of early successional plant communities (Leopold 1933; Rosene 1969; Brennan et al. 2014). Lusk et al. (2002) used Texas Department of Agricultural Statistics data from 1978 to 1997; this captures the temporal shift from smaller farms with brushy cover to large-scale clean farming. Lusk et al. (2002) demonstrated that northern bobwhite abundance in Texas increased by 25% as cultivation increased to 20%. Beyond 20% cultivated, northern bobwhite abundance decreased. The removal of weeds and the use of herbicides have had negative effects on northern bobwhites (Klimstra 1982; Brennan 1991; Hernández et al. 2012; Evans et al. 2013).

### County scale patterns

The county-scale analysis provided empirical evidence to incorporate the domain of scale concept when dealing with multiple scales in northern bobwhite studies. We found similar results across the three different extents used at this scale continuum, suggesting that these three extents representing northern bobwhite metapopulations are potentially within the same domain of scale. Although this is an initial analysis, it provides an improved understanding of landscape changes across scales and the building of multiscale predictive models for wildlife habitat (Wheatley 2010).

Road density was higher for populations with declining abundance, compared with populations with stable abundance. This suggests that roads may be negatively affecting northern bobwhite populations, potentially by fragmenting larger patches of habitat. Road density and its correlate, human development, may affect northern bobwhite population density. For example, in a study in Delaware, northern bobwhite presence was negatively related to cohesive patches of human development within 2.5 km (Duren et al. 2011).

Northern bobwhite populations benefitted from smaller, yet more connected, patches of pasture. Pasture provided grasses and some woody cover; however, this suggests large patches of pasture are less suitable for northern bobwhite. Across the range of northern bobwhite, the successional stage preferred by the species is variable with rainfall, soil type, length of growing season (Guthery and Brennan 2007). Thus, northern bobwhites may prefer early successional vegetation, dominated by grasslands (Twedt et al. 2007; Janke and Gates 2013) and mid- to late successional stages of vegetation (Spears et al. 1993; Duren et al. 2011). These preferences can shift through the seasons; brooding hens may select sites with more forbs and taller vegetation, while roosting and nesting hens choose taller grasses (Taylor et al. 1999).

Northern bobwhite population abundance was higher where woody cover occurred in larger patches, suggesting that smaller patches of woodland with more edge were less suitable for northern bobwhite. This is supported by Janke and Gates (2013), who found that while woody cover accounted for 11–17% available habitat, it supported 49% of the covey locations. Brooding, nesting, and roosting northern bobwhites selected sites with more cover (Taylor et al. 1999), and Duren et al. (2011) found a weakly positive relationship of northern bobwhite presence and percent forest within 1 km of their sampling points. Northern bobwhites in Georgia preferred open pine canopy, near oil fields, and early succession of habitat, as opposed to dense forest (White et al. 2005). O’Connor et al. (1999) found that...
habitat patch size and configuration became especially important in areas where cropland and woodland replaced native prairie.

Northern bobwhite abundance was lower where cropland patches were smaller. This coincides with other studies that have found a trend between northern bobwhite populations and cropland. Janke and Gates (2013) found that while cropland accounted for 28–38% available habitat, it had only 5.5% of the covey locations. Similarly, Twedt et al. (2007) found that in the West Gulf Coastal Plain, detections were greater where cropland was aggregated. Duren et al. (2011) found that northern bobwhite populations were negatively related to crop cover edge density. More detailed land-cover metrics may be affected by scale; small patches may be favored in northern bobwhite habitat but cannot be detected at 30-m resolution.

Local scale analysis

Northern bobwhite populations with stable abundance in Texas and Oklahoma had significantly more woody vegetation in larger patches, spread further apart, and less herbaceous habitat in smaller patches. The association with woody cover has been noted on studies with a similar scale. Janke and Gates (2013) found that northern bobwhites showed less preference for grasslands and instead selected early succession woody habitat. Configuration of the woody cover is also important: Brooke et al. (2015) found that distance to shrub cover was an important factor for macrohabitat selection of northern bobwhites in the breeding season. Duren et al. (2011) found that northern bobwhite populations were negatively related to interspersion, juxtaposition, and edge density of early successional habitat. The relationship with woody cover noted in our study, while not surprising, was less discernable at larger spatial scales partially because of the resolution at those scales.

It is worth noting that analyses at the county and local scales were focused on current vegetation types, rather than changes in vegetation over time. Thus, our comparisons of vegetation between counties and parishes with declining and stable northern bobwhite populations is limited to one point in time. We recommend future research on land use and vegetation types over time at these spatial scales.

Management Implications

This hierarchical analysis provided a framework to provide information for management at multiple spatial scales. We concluded that at the regional and metapopulation persistence scale, providing pasture and rangeland habitat with a percentage of woodland in a connective pattern for movement corridors was important for mitigating against the effects of urbanization. At the local, or pasture, scale, our results indicate the rancher and landowner may improve northern bobwhite abundance by focusing on providing woody cover with smaller patches of herbaceous and bare ground.

Supplemental Material

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Table S1. Comparison of road density and 2013 class-level landscape metrics in counties with declining and stable northern bobwhite Colinus virginianus abundance. Counties with declining abundance included Erath, Fisher, and Jim Hogg in Texas, and Grady, Love, and Osage in Oklahoma (TX/OK – ). Counties with stable abundance included Donley, Frio, and Refugio in Texas, and Grant, Pushmataha, and Roger Mills in Oklahoma (TX/OK + ). Ten random points/county were sampled at three buffer sizes that represented 95% metapopulation persistence, two of which are shown in this table (8, 50 km²). Statistics in bold are significant ($p = 0.05$).

Table S2. Road density and 2013 class-level landscape metrics in Louisiana parishes with declining northern bobwhite Colinus virginianus abundance. Parishes included Calcasieu, Franklin, Jackson, St. Tammany, Union, and Vernon. Ten random points/parish were sampled at three buffer sizes that represented 95% metapopulation persistence: 8, 50, and 96 km².

Table S3. Class-level landscape metrics for 2014 in Louisiana parishes with declining northern bobwhite Colinus virginianus abundance. Parishes included Calcasieu, Franklin, Jackson, St. Tammany, Union, and Vernon. Twenty-five random points per county were sampled at 0.15 km², representing northern bobwhite home range.

Figure S1. Northern bobwhite Colinus virginianus abundance in Texas, Oklahoma, and Louisiana, 1970–2010. Routes were obtained from the North American Breeding Bird Survey, through 2014, and for 1972–2012 the value is represented as a 5-y rolling average (e.g., 1972 is an average of 1970–1974).

Figure S2. Percentage of pasture and rangeland, woodland, and cropland for 1974–2012 (data for 1978–1997 obtained with permission from Okay 2004).

Reference S1. Coffey L, Baier AH. 2012. Guide for...
organic livestock producers. U.S. Department of Agriculture.

Found at DOI: https://doi.org/10.3996/112017-JFWM-094.S5 (14.09 MB PDF); also available: https://www.ams.usda.gov/sites/default/files/media/GuideForOrganicLivestockProducers.pdf.

Reference S2. Daigle JJ, Griffith GE, Omernik JM, Faulkner PL, McCulloh RP, Handley LR, Smith LM, Chapman SS. 2006. Ecoregions of Louisiana (color poster with map descriptive text, summary tables, and photographs): Reston, Virginia, U.S. Geological Survey (map scale 1:1,000,000).

Found at DOI: https://doi.org/10.3996/112017-JFWM-094.S6 (15.84 MB PDF); also available: ftp://newftp.epa.gov/EPADataCommons/ORD/Ecoregions/la/la_front.pdf.

Reference S3. Woods AJ, Omernik JM, Butler DR, Ford JG, Henley JE, Hoagland BW, Arndt DS, Moran BC. 2005. Ecoregions of Oklahoma (color poster with map, descriptive text, summary tables, and photographs): Reston, Virginia, U.S. Geological Survey (map scale 1:1,250,000).

Found at DOI: https://doi.org/10.3996/112017-JFWM-094.S7 (16.09 MB PDF); also available: ftp://newftp.epa.gov/EPADataCommons/ORD/Ecoregions/ok/ok_front.pdf.

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