Research Article

Increasing and Declining Populations of Northern Bobwhites Inhabit Different Types of Landscapes

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Abstract

*Northern bobwhites (*Colinus virginianus*) have been declining in abundance throughout their range for several decades, and perhaps a century. Although wildlife biologists are well aware of this trend, most attempts to understand the declines have examined only a few local populations in a limited geographic area or have examined declines at a very large scale without reference to specific populations. Few studies use a standard protocol for examining trends in local populations throughout the entire natural range of bobwhites. I used the National Resources Inventory, a geographically extensive and intensive database on land cover and use, to characterize the composition and heterogeneity of landscapes inhabited by bobwhite populations that have been increasing (43 populations), decreasing (468), or become locally extinct (28). I tested bobwhite populations for overall positive or negative change, over the past 10 years or more, using data from the North American Breeding Bird Survey and a randomization test that controls for observer effects. Landscapes occupied by increasing and decreasing populations were, on average, different from one another in composition but not heterogeneity. As predicted, landscapes of decreasing populations tended to have a greater percentage of nonuseable land (e.g., urban and forestland) and a lesser percentage of useable land (e.g., cropland, pastures, and rangeland) as compared to landscapes where bobwhites actually increased. Moreover, landscapes where bobwhites had recently become extinct were different from those where bobwhites were only declining. In particular, a very large percentage of urban land characterized the landscapes of extinct populations. To some extent, landscapes of large (above average) and small (below average) populations also differed as predicted. The results do not point to a single universal explanation for bobwhite declines, but they do clearly show that declining populations inhabit local landscapes that, on average, are very different from those occupied by increasing populations. This knowledge may assist quail biologists and land managers to recognize the general type of landscape where the restoration of bobwhites may be most successful and where extant populations may be most threatened.* (JOURNAL OF WILDLIFE MANAGEMENT 70(4):922–930; 2006)

Key words

Colinus virginianus, *cropland, landscape composition, National Resources Inventory, North American Breeding Bird Survey, northern bobwhites, population, urbanization.*

For several decades now, northern bobwhites (*Colinus virginianus*) have been declining in abundance throughout many areas of their natural range in the eastern, central, and southern United States (Brennan 1991, Church et al. 1993, Burger 2002, Dimmick et al. 2002, Lusk et al. 2002, Williams et al. 2003, Sauer et al. 2004). The declines may have started more than a century ago (Stoddard 1931). The primary cause of these declines has been the large-scale deterioration of bobwhite habitat due to succession advancing to a closed-canopy climax state, intensive monoculture farming, and intensive timber management (Burger 2002). Although other more specific causes of local declines vary regionally, the combined effect has been a decrease of landscape space available for bobwhites (Guthery 1997). Because of many studies of local bobwhite populations, wildlife biologists recognize the importance of landscape composition to population dynamics. However, no study has yet documented the relationship between landscape composition and local population dynamics for a geographically widespread set of populations. Previous studies have been limited either in geographic scope or in local detail. Examples of the latter include studies that examine site-specific factors affecting the dynamics of one or a few local bobwhite populations (e.g., Roseberry and Klimstra 1984, Taylor et al. 1999*a*, Williams et al. 2000). Examples of the former include studies that examine broad geographic factors as they affect the general average trajectory of bobwhite populations within an ecoregion or other large land area (e.g., Church et al. 1993, Lusk et al. 2002, Peterson et al. 2002, Williams et al. 2003). Studies of both types have been crucial in contributing to our current understanding of the autecology, population biology, and conservation status of bobwhites.

However, there is a need for studies that examine the effect of local factors, natural and anthropogenic, on local populations (e.g., Roseberry and Sudkamp's [1998] study in Illinois) throughout the entire natural range of bobwhites. Such a study would have the advantages of being both intensive and extensive; it could examine the local factors immediately affecting bobwhite populations, and at the same time have a broad geographic scope by including many widely scattered populations. Moreover, the study would ideally have a standard sampling protocol for determining the trends of local bobwhite populations and for quantifying the local ecological and anthropogenic factors potentially affecting each population. I undertook such a study by comparing the landscapes of increasing bobwhite populations to those of decreasing populations. I examined over 500 bobwhite populations.

Specifically, I wanted to determine if declining and increasing populations inhabit fundamentally different landscapes with regard to land composition and heterogeneity. In general, bobwhites prefer relatively open habitat that includes a mix of shrubs, grasses, forbs, and bare ground; this mix facilitates nesting, brood-rearing, and foraging (Stoddard 1931, Wilkins and Swank 1992, Barnes et al. 1995, Taylor et al. 1999*b*, Cram et al. 2002). I identified 3 general landscape cover types assumed to be favorable or beneficial to bobwhite populations: cropland,

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pastureland, and rangeland. The National Resources Inventory (NRI) defines rangeland as land where the vegetation is primarily native grasses, forbs, and low shrubs existing as the climax successional state or as an earlier successional state maintained by burning, chaining, and rotational livestock grazing. A common feature of cropland, pastureland, and rangeland is the presence of ground cover without a dense canopy overhead. I also recognized 3 general landscape cover types assumed to be of little use to bobwhite populations: forest, urban land, and water. These 3 cover types either lack resources for nesting and feeding or have a dense canopy that could obstruct escape from predators. I predicted that declining populations of bobwhites inhabit landscapes that have smaller proportions of the first 3 cover types and have greater proportions of the latter 3 cover types than the landscapes occupied by increasing populations of bobwhites. I tested these predictions at 2 spatial scales (i.e., 2 landscape sizes) to determine whether my results were independent of spatial scale. I expected the same results at each scale even though the smaller landscapes were only 4% of the size of the larger landscapes.

I also predicted that declining populations of bobwhites inhabit landscapes that are less heterogeneous (with regard to the 6 cover types) than the landscapes occupied by increasing populations. Previous studies have suggested that landscape or habitat heterogeneity is beneficial to bobwhites (Brady et al. 1993, Roseberry and Sudkamp 1998). Heterogeneity often entails the existence of a patchy landscape with a moderate cover of row crops and pasture, along with brush fencerows and abandoned cropland in the early stages of succession; all of which can be utilized by bobwhites (Rosene 1969, Roseberry and Klimstra 1984, Brennan 1991). The observation that bobwhites benefit from a patchy, heterogeneous landscape led Brennan (1991) to suggest that decades-long declines in bobwhite populations have been due, in part, to a trend toward increasingly cleaner farming (i.e., larger crop fields, few hedgerows, and greater herbicide and pesticide usage); Stoddard (1931) made a similar observation. Although the land cover data did not allow me to identify areas of clean farming, I quantified the heterogeneity of a landscape as the number of different land cover types represented along randomly placed transects (see Methods). According to Brennan (1991), a major land conversion toward cleaner farming or a less heterogeneous mix of land cover types could adversely affect bobwhites and other species with similar habitat requirements (Brady and Flather 1998, Dimmick et al. 2002, Murphy 2003, Peterjohn 2003). Studies of the landscape-level factors affecting bobwhite populations are pertinent because bobwhites are an important game species with economic value (Burger et al. 1999) and may be a sentinel species that is particularly sensitive to certain types of anthropogenic changes in the landscape that will also negatively affect other bird species.

Study Area

The study area included most of the eastern and central United States where northern bobwhites occur. More specifically, I examined bobwhite populations occurring on local survey routes of the North American Breeding Bird Survey (see below).

Methods

Determining the Direction of Change in Bobwhite Populations

I used data from the North American Breeding Bird Survey (USGS Patuxent Wildlife Research Center 2003) to identify increasing and declining populations of bobwhites. The Breeding Bird Survey (BBS) is an annual survey of birds seen or heard along more than 3,000 routes throughout the United States, Canada, and Mexico. The survey has been ongoing since 1966. A single observer drives each 39.4-km route and records the numbers of individuals of each species at stops every 0.8 km along the route for 50 stops. More details of the sampling design can be found in Robbins et al. (1986), Droege and Sauer (1990), Peterjohn and Sauer (1993), Sauer et al. (1994), or at the website (<http://www.mbr-pwrc.usgs.gov/bbs/>; Sauer et al. 2004). I limited my analyses to populations within the natural or historic geographic range of bobwhites. I did not include introduced populations of bobwhites in the western states. I use the term *population* as a convenient label for the birds recorded on a route (other authors have used the phrase *index of abundance*), though population in this sense does not necessarily signify a single closed or complete population. That is, although bobwhites are relatively sedentary, I cannot be completely certain that a BBS route actually samples only one population and that adjacent routes do not sample the same metapopulation. Williams et al. (2003) also used the term *population* to refer to bobwhites counted along routes in a similar survey. Whether counts of bobwhites along a BBS route represent a true population does not directly affect my analyses; the important assumption is that the size of the landscapes (25-km- and 5-km-radius circles; see below) are appropriate for examining the relationship between bobwhite abundance and landscape composition.

I first identified the BBS routes in which bobwhites were recorded for at least 10 years between 1966 (the first year of the BBS) and 1999 and for at least 3 years between 1995 and 1999 (a 5-yr time span centered on 1997, the year that the NRI land cover data were compiled). More than 1,200 BBS routes met these 2 criteria. From this initial group of over 1,200 BBS routes (or bobwhite populations), I then identified and selected the populations that were significantly increasing and those that were significantly declining ($P < 0.05$), based on annual abundances estimated between 1966 and 1999. I devised a randomization test that controlled for the observer effect (known to exist in BBS data; see Sauer et al. 1994, Link and Sauer 1998) and enabled testing for significant population trends within routes (Appendix). The randomization test has good power for 10 or more years of data. Many, if not all, previously developed methods for analyzing BBS data involve testing for significant population trends above the level of individual BBS routes (Robbins et al. 1989, Link and Sauer 1994, 1997, 1998, James et al. 1996, Thomas 1996). In my study, it was necessary to test for statistical significance at the route level. I used the randomization test to find the BBS routes in which bobwhites were either significantly increasing or decreasing between 1966 and 1999 (Appendix). I found 767 such routes. I selected routes for further analysis if land cover data from the NRI (see below) adequately described the surrounding landscape.

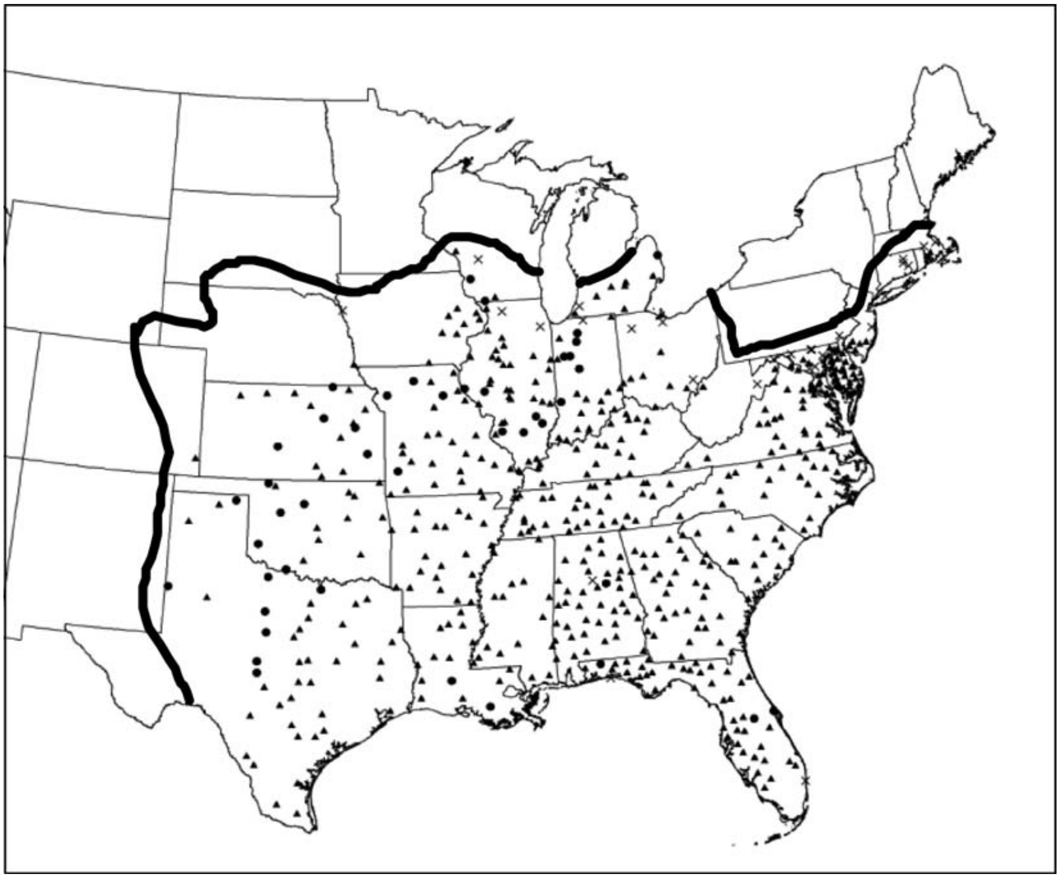

Figure 1. The natural geographic range of northern bobwhites and locations of the Breeding Bird Survey (BBS) routes (bobwhite populations) within the central and eastern United States. Circles represent BBS routes where bobwhites were increasing in abundance, triangles represent decreases in abundance, and "X" indicates local extinction between 1966 and 1999. Heavy line represents the edge of the geographic range.

There were 511 (of the 767) routes that met this requirement (Fig. 1).

I divided the 511 bobwhite populations (or routes) into 2 groups. One group of 43 included bobwhite populations that were significantly ($P < 0.05$) increasing, while the second group of 468 included those populations that were significantly decreasing, as identified by the randomization test. I also derived a third group of 28 routes where bobwhites had recently become locally extinct (Fig. 1). I defined the condition of *locally extinct* by the absence of bobwhites on the route since 1995 (or a previous year) after 10 or more years of recorded bobwhite abundance prior to 1995 (or the first year of absence). Thus, I had 3 groups representing populations that were increasing, decreasing, or locally extinct.

In a separate analysis, I divided the 511 bobwhite populations into 2 groups representing populations with greater than average abundance (196 BBS routes) and less than average abundance (315 BBS routes). I defined *average abundance* as the mean number of individuals per route (for all 511 routes) per year for the period 1995 to 1999 (16.2 individuals).

Quantifying the Characteristics of Landscapes

For each of the 539 BBS routes, I characterized the landscape within a 25-km-radius circle surrounding and completely encompassing the route. I used land cover data from the 1997 NRI, a database compiled by the Natural Resources Conservation Service of the United States Department of Agriculture. The NRI is an inventory of soil, water, land cover or use, and related data on nonfederal land within the United States. The NRI consists of more than 800,000 sample points arranged in a stratified clustered random design. More detail on the sample design and protocol for the NRI can be obtained in Nusser and Goebel (1997), Nusser et al. (1998), Breidt and Fuller (1999), and Natural Resources Conservation Service (2000). On average, there were 319 NRI points within the circular landscape scenes centered on the BBS routes and the number of points ranged from 100 to 945. In previous unpublished analyses, I found that 100 or more points were sufficient to adequately characterize the landscape. These analyses were based on counties as landscapes where the exact amount of each land cover type in a county was known; the method (described below) typically estimated the proportions of 6 general land cover types (see below) to within 94–106% of their actual values.

An X-shaped transect (each arm is 152.5 m) was centered on each NRI point (Natural Resources Conservation Service 1997). I used the proportion of the transect represented by each of 6 general landscape cover types to estimate the percentage of each land cover type at the point. The land cover types are cropland, pastureland, rangeland, forest, artificial and barren land, and water (Table 1; Natural Resources Conservation Service 1997). The artificial and barren land cover type mostly consists of urban and suburban development, but also includes roads, highways, and buildings in rural areas. I obtained relative estimates of the

Table 1. The 6 land cover types used to characterize landscapes of populations of northern bobwhites in the United States that were either increasing or decreasing between 1966 and 1999.

Cover type[a]	Description
Cropland	Annually cultivated crops and their winter residue
Pastureland	Perennial and annual herbaceous vegetation (pastures and hayfields)
Rangeland	Open-canopy woody vegetation with 5–25% canopy coverage, mostly grass and forbs
Forest	Closed-canopy woody vegetation with >25% canopy coverage
Artificial and barren land	Urban, suburban, farmsteads, land used for transportation; barren land without vegetation, such as unreclaimed mined land
Water	Large and small permanent water bodies (streams, rivers, ponds, lakes). Cover type does not include wetlands

[a] The National Resources Inventory of 1997 actually recognizes 9 cover categories for land sampled by the X-transect. I combined pairs of some these categories into 1 cover type. Thus, forest represents any type of vegetation with a closed canopy, regardless of height. Pastureland may include some land that would be classified as rangeland in other land classification schemes. I combined 2 categories when I assumed them to have the same effect on bobwhite population dynamics.

amount of land cover of each type in each circular landscape scene by calculating, for each cover type, the mean percent cover over all points. I emphasize that this method of characterizing the landscape does not provide estimates of the absolute amount of land of each cover type as either a percentage or a raw value. Each NRI point has an associated expansion factor that quantifies the amount of land that the point represents (Nusser and Goebel 1997, Nusser et al. 1998). However, these expansion factors are only valid for sampling units that are based upon the NRI sample frame (aggregation of county boundaries and 4-digit hydrologic cataloging units); therefore, I could not use them. I provided estimates of land cover that are relative to one another within a landscape scene to characterize the landscapes. For example, if forestland occupies an average of 50% of each X-transect and cropland only occupies 10%, then I deduced that there is more forestland than cropland in that landscape scene.

The NRI points enabled me to characterize landscape configuration or heterogeneity as well as composition. Each X-transect provides proportions, p_i, for each of the general cover types $(i = 1, \ldots, 6)$. Therefore, I was able to calculate estimates for land cover heterogeneity at each NRI point by using 2 well-established indices. I calculated the index of cover dominance (COVD; O'Neill et al. 1988) as $\mathrm{COVD} = [\ln(n) + \sum p_i \ln(p_i)]/\ln(n)$, where n equals the number of cover types on the transect. The COVD ranges between 0 and 1. Large values of COVD indicate a landscape with little heterogeneity where 1 or 2 types of land cover dominate; small values indicate a heterogeneous landscape where many land cover types exist in roughly equal proportions (O'Neill et al. 1988). The number of segments per X-transect (SEGM) was simply the number of linear segments of different cover types on the transect, without regard for type of land cover. The maximum value for SEGM was 200, given that the recorded changes in land cover along the X-transects occurred at a maximum resolution of 3.55 m. The SEGM is similar to the interspersion index (Baxter and Wolfe 1972) and the patch-per-unit index (Frohn 1998). An increase in SEGM indicates increasing heterogeneity. For each NRI point, I obtained COVD and SEGM. Using all the points within a landscape scene, I then calculated the mean COVD and SEGM for each landscape scene.

The land cover data characterize the landscapes as they appeared in 1996–1997 (the year of the NRI that provided the data), while the data for calculating bobwhite population trends extend as far back as 1966 for some populations. Thus, there may appear to be a mismatch between the 2 data sets, in that the population data cover a longer time span than do the land cover data. For each BBS route, I decided to use as many years of data as were available because the randomization test has increasing power for detecting real population trends as the amount of data increases. Moreover, population trends over the longest possible time span (34 years, 1966–1999) tended to be in the same direction (increasing or declining) as more recent trends (e.g., 1995–1999), though the latter were not always significant due to low power. Furthermore, 30-year changes in landscape composition have probably been relatively gradual and consistent when they occurred. I assume that the population trends of bobwhites reflect the response of the populations to landscape composition in the past as well as the present (1996–1997) and that past landscapes were not radically different from the ones characterized by the 1997 NRI data.

Testing for Differences between Landscapes

I examined whether increasing, decreasing, and extinct populations of bobwhites occupy landscapes of different land cover composition and heterogeneity. For each of the 6 land cover types and 2 indices of landscape heterogeneity, I first tested whether the group of increasing populations occupied landscapes that were significantly different (i.e., either greater than or less than, depending on the land cover type) from the group of decreasing populations. When significant ($P < 0.05$), I then tested for differences between the group of decreasing populations and the group of locally extinct populations. The groups tended to have unequal variances for most of the 8 landscape variables, perhaps due to unequal sample sizes. Because of this heteroscedasticity, I used Welch's approximate t-test (Sokal and Rohlf 1995) for all comparisons.

I also assessed whether bobwhite populations with greater than average abundance occupy landscapes that differ from the landscapes occupied by populations with less than average abundance. Thus, I tested for a significant difference between those 2 groups for each of the 6 land cover types and the 2 indices of heterogeneity using Welch's approximate t-test.

Testing for an Effect of Scale

In order to expand the scope of inference from my study, I examined whether I could obtain the same results at a smaller spatial scale (i.e., less extensive bobwhite populations inhabiting smaller landscapes). I tested for an effect of spatial scale on the differences between landscapes where bobwhites were increasing and those where they were decreasing. I used the same protocol as described above, except that I categorized bobwhite populations as either increasing or decreasing based on data recorded for the middle fifth of each BBS route (i.e., stops 21 to 30 spanning a distance of 7.2 km). Thus, from the group of 511 routes I obtained a subset of 415 routes that had bobwhite populations that were

Table 2. Landscapes in which northern bobwhite populations were increasing (I), decreasing (D), or locally extinct (E) within the United States between 1966 and 1999.

Landscape variable	Mean			D vs. I			E vs. D		
	I	D	E	df[a]	*t*	*P*	df[a]	*t*	*P*
Cropland	37.8	18.8	19.2	49	−5.23	<0.0001	30	0.09	0.4632
Pastureland	25.9	20.0	12.1	47	−2.09	0.0208	43	−5.26	<0.0001
Rangeland	8.9	4.4	2.1	43	−1.71	0.0476	51	−4.15	<0.0001
Forest	18.1	44.8	32.9	61	10.46	<0.0001	30	−2.65	0.0064
Urban	6.9	8.7	29.4	57	1.68	0.0494	27	5.03	<0.0001
Water	2.7	3.7	4.6	56	1.67	0.0790			
Cover dominance	0.609	0.608	0.612	47	−0.05	0.4813			
Segments	4.69	4.71	4.75	47	0.15	0.4406			

[a] Degrees of freedom in Welch's approximate *t*-test are a function of both the sample size and the variances of the 2 groups.

either significantly increasing (29) or decreasing (386). Note that I did not define a group of locally extinct populations in this analysis, as I was not confident that information from only 10 stops could determine local extinction at such a small scale.

I used data from the 1997 NRI to characterize the landscapes surrounding the middle portion of each BBS route. The landscapes were circles with a radius of 5 km and typically contained 10–20 NRI points. I used paired-comparisons analyses of variance (ANOVAs; the 25-km and 5-km landscapes for a route formed a pair, $n = 415$) to test for differences between the 25-km- and 5-km-radius landscapes for each of the 8 landscape variables. The ANOVAs were direct tests of whether the 25-km and 5-km landscapes were different, regardless of whether the landscapes contained increasing or decreasing bobwhite populations. When the landscapes had different values for a landscape variable, I applied Welch's *t*-test to test for a significant difference between the landscapes of increasing and decreasing populations.

Results

Of the more than 500 bobwhite populations that I examined, only 43 populations were increasing over the last few decades. Declining populations of bobwhites occupied 25-km landscapes that were significantly different from those landscapes occupied by increasing populations, for 5 of the 6 cover types (Table 2). As predicted, declining populations inhabited landscapes with less cropland, pastureland, and rangeland, and more forestland, and artificial and barren land than the landscapes of increasing populations (Table 2). The relative proportion of water was, on average, small and not different between the 2 types of landscape ($P = 0.079$). Furthermore, landscapes where populations had recently become extinct differed in some ways from landscapes where populations were only declining. The former landscapes had relatively less pastureland and rangeland and had much more artificial and barren land (Table 2). The compositional heterogeneity (as measured by cover dominance and number of segments on an X-transect) of landscapes occupied by increasing and decreasing populations was remarkably similar (Table 2).

Bobwhite populations with less than average abundance occupied landscapes that were significantly different from those landscapes occupied by populations with greater than average abundance. As I predicted, the former landscapes had less cropland, pastureland, and rangeland, and had more forestland, artificial and barren land, and water than did landscapes inhabited by large populations (Table 3). In addition, large populations inhabited landscapes that had greater compositional heterogeneity (as measured by cover dominance, recall that heterogeneity increases as cover dominance decreases) than the landscapes occupied by small populations (Table 3).

There was virtually no effect of spatial scale on the above results for population trend, perhaps because most 25-km- and 5-km-radius landscapes did not differ much in any of the 8 landscape variables (results of the paired-comparisons ANOVAs did not reveal significant differences). Therefore, differences in the composition of 5-km-radius landscapes occupied by declining and increasing populations were very similar to the differences found in 25-km-radius landscapes. For increasing populations, 5-km-radius and 25-km-radius landscapes had 31% and 37% cropland, and 24% and 18% forestland, respectively, and had

Table 3. Landscapes in which northern bobwhites had greater than average and less than average abundance within the United States between 1966 and 1999.

Landscape variable	Mean		Greater than vs. less than average		
	Greater than average	Less than average	df[a]	*t*	*P*
Cropland	24.8	17.7	442	−3.60	0.0002
Pastureland	22.4	19.3	373	−2.20	0.0143
Rangeland	5.8	4.2	307	−2.03	0.0217
Forest	37.3	45.8	437	4.11	<0.0001
Urban	6.9	9.5	509	3.85	<0.0001
Water	3.1	4.0	478	1.74	0.0416
Cover dominance	0.591	0.619	449	3.29	0.0005
Segments	3.1	4.0	452	−1.08	0.1340

[a] Degrees of freedom in Welch's approximate *t*-test are a function of both the sample size and the variances of the 2 groups.

differences of 3% or less for the other cover types and for the 2 indices of heterogeneity. Differences in cover type and heterogeneity were never greater than 2% for 5-km-radius and 25-km-radius landscapes occupied by decreasing populations. Spatial scale also had almost no effect on determination of population trend. That is, except for 1 BBS route, there were no instances of cross-classification whereby a population that was significantly increasing over the entire route (stops 1–50) was found to be significantly decreasing within the middle of the route (stops 21–30), or vice versa. Granted, there were many routes for which the randomization test was not powerful enough to detect significant increase or decrease based only on the middle 10 stops.

Discussion

The objective of my study was to determine if bobwhite populations that are increasing inhabit different types of landscapes than do populations that are declining. I predicted that increasing populations should inhabit landscapes with more beneficial land cover and less detrimental land cover. As predicted, increasing populations of bobwhites inhabit landscapes that are quite different from the type of landscapes occupied by declining populations. Landscapes of increasing populations have more cropland, pastureland, and rangeland, all of which are favorable to the reproduction of bobwhites. Furthermore, landscapes of recently extinct populations have even less of these favorable types of land cover. In general, cropland, pastureland, and rangeland together must compose more than half of a landscape in order to sustain populations of bobwhites. As a corollary to this, cover types that are not favorable to bobwhites (e.g., forest, urban land, and large water bodies) must be limited in landscapes to sustain populations of bobwhites. Increasing populations occupy landscapes with substantially less forestland than the landscapes of decreasing and recently extinct populations. Although open-canopy woodlands and woody fencerows provide desirable bobwhite cover, large blocks of forest do not. Wellendorf et al. (2002) reported that covey use within forested and fallow blocks was concentrated along edges of crop fields, leaving large portions of this habitat type unused. Urban land is also much more common in landscapes where bobwhites have recently become extinct than in landscapes where bobwhites are still extant, even if they are currently declining.

The difference in urban land between landscapes of decreasing and extinct populations is one of the more profound results of my study. Although there are several excellent studies of the effect of landscape composition on the population trends of bobwhites (Brady et al. 1993, Guthery et al. 2001, Peterson et al. 2002), few studies include urban land as a cover type (Brady et al. 1998, Roseberry and Sudkamp 1998). Thus, the documented effects of urbanization (a ubiquitous and major trend in land use) on bobwhite populations are not as extensive as the documented effects due to other land uses. At a much larger spatial scale than that of my study, Brady et al. (1998) found a negative correlation between the amount of urban land in Major Land Resource Areas (ranging in size from 10,000 to 285,000 ha) and bobwhite population trends. Roseberry and Sudkamp (1998) included data on urban land cover, though it was not included in their final landscape suitability model for bobwhites in Illinois. To date, my study may provide the clearest indication of the effects of urban land on bobwhite population trends. As the relative percentage of urban land in a 2,000-km^2 landscape approaches 30%, bobwhites are likely to become locally extinct, particularly if the proportion of useable land is low (e.g., <50% cropland, pasture, and rangeland). It is clear that increasing populations of bobwhites inhabit landscapes where the amount of urban land is limited. Of the 43 bobwhite populations exhibiting an increase in population, 37 populations occupied landscapes with <10% urban land. This negative effect of urbanization is not limited to just the outward expansion of cities and towns associated with commercial and industrial development. My definition of urban land (the artificial and barren land cover type of the NRI) includes high-density housing in suburban areas and neighborhoods that retain some natural landscaping on relatively large and widely spaced lots. Thus, even land development presumed to be eco-friendly might be associated with declines in bobwhite populations.

The negative effect of urban land is probably due to bobwhites' inability to use land so far removed from a natural state. There are many different types of land cover that bobwhites can use to some extent during at least one season of the year. The useable space hypothesis (and management strategy) suggests that the most critical factor for maintaining and enhancing a bobwhite population is the amount of landscape that is "compatible with the physical, behavioral, and physiological adaptations of bobwhites in a time-unlimited sense" (Guthery 1997:292). According to this hypothesis, habitat interspersion and landscape heterogeneity are not as important (Guthery 1997, Guthery et al. 2001). Overall, the results support this hypothesis in that the mean landscapes of increasing, declining, and extinct populations of bobwhites had approximately the same amount of compositional heterogeneity (Table 2). On the other hand, large populations tended to occupy landscapes with greater heterogeneity (as measured by cover dominance) than the landscapes occupied by small populations (Table 3). Thus, landscape heterogeneity may be important to actual population size (as a long-term average) even if it does not influence temporal changes in population size (i.e., population trajectories).

The useable space hypothesis and other studies identify cropland as a cover type of potential use to bobwhites (Guthery et al. 2001, Lusk et al. 2002), though not all crops are useful (Brady et al. 1993, Peterson et al. 2002). In addition, there may be intermediate levels of cultivation that are optimal for bobwhite population maintenance and growth. In some midwestern states, e.g., Illinois and Missouri, bobwhite abundance (at a county level) is greatest when 30–60% of the county is under cultivation (Dailey 1989, Roseberry and Sudkamp 1998). As for trend in bobwhite populations, my results indicate that increasing populations inhabit landscapes that were composed of an average of 38% (cropland only) to 64% (cropland and pastureland) agricultural land. However, it is premature to conclude that this represents an optimal range of agriculture. My analysis included populations (BBS routes) throughout the range of bobwhites; the optimal landscape composition for each local population is likely to vary widely. Guthery (1999) reported that many different patch configurations might lead to optimal landscapes for bobwhites, a property of the bobwhite–habitat interface defined as *slack*.

Moreover, various local factors (e.g., weather, hunting pressure, predators) unrelated to landscape composition are likely to affect the dynamics of each local population.

It is reasonable to assume that a myriad of site-specific and interrelated factors affect the dynamics of bobwhite populations. Because of this, it is not surprising that biologists have not found a clear and simple relationship between any one factor (or causative agent) and long-term population dynamics that holds true for bobwhite everywhere. Peterson et al. (2002) conducted a data-intensive and extensive analysis using spatially interpolated estimates of bobwhite abundance and landscape composition for 100,000 randomly selected points throughout the range of bobwhites. Although there were spatial and temporal patterns in land covered by cropland, rangeland, and woodland, these patterns were not always congruent with spatial and temporal patterns of bobwhite abundance (Peterson et al. 2002). Studies employing regression-based analyses may not always be the best choice for examining the relationship between landscape variables (or other types of variables) and bobwhite abundance or population trends. The large amount of scatter (error variance) in such relationships (e.g., Brady et al. 1998, Roseberry and Sudkamp 1998, Peterson et al. 2002) may obscure other patterns in the data. For example, I always obtained small correlation coefficients ($-0.08 < r < 0.08$) when I regressed bobwhite population trend and proportions of the different land cover types for the 539 landscapes of my study (analysis not presented). However, as indicated by my results, there are definite differences in land cover composition between landscapes where bobwhites are increasing and those where they are decreasing. This distinction between landscapes was made clear only when I ignored variation among all 539 landscapes and instead focused my attention on average differences between landscapes assigned to 1 of 3 groups: increasing, decreasing, and extinct populations. Granted, the variance within a group did influence the outcome of the *t*-tests.

To improve my study, I would use data on trends in land cover or use as well as trends in bobwhite populations. The land cover data were static estimates obtained from the 1997 NRI. Some types of land cover (e.g., urban land) have increased dramatically in the last several decades. The effect of urbanization on bobwhite populations is best addressed using data on temporal changes in the amount of urban land, at a range of spatial scales. In addition, some general cover types (e.g., cropland) can be further subdivided to get a more refined analysis of their effects on bobwhite populations (Brady et al. 1993, 1998, Peterson et al. 2002). Some types of crops may benefit bobwhites (e.g., sorghum, oats, wheat), whereas others (e.g., cotton) probably do not. Other authors have emphasized the need for field data at finer scales (DeMaso et al. 2002) or multiple scales (Kuvlesky et al. 2002). I used coarse-scale descriptions of cover types to assess trends across the full geographic range of bobwhites. Subtle changes in land use, not easily detected with remote sensing, may substantially alter the carrying capacity of some landscapes occupied by bobwhites (Roseberry 1979).

In summary, landscape-level studies of the factors affecting bobwhite populations will probably not lead to a precise, all-encompassing strategy for management. However, such studies do have the potential to inform biologists and land managers as to what general type of landscape best benefits bobwhites.

Management Implications

Agriculture and forestry are the 2 main uses of the rural land throughout the range of bobwhites. My results further support the conclusion that one of these economic pursuits (i.e., forestry) may not be conducive to the viability of bobwhite populations, although the other (i.e., agriculture) can be in some circumstances. In recent years the management of bobwhites living on agricultural lands has been encouraged through the Conservation Reserve Program, the Conservation Security Program, and related programs of the United States Department of Agriculture. These programs provide financial incentives for landowners to manage their land as wildlife habitat. However, my study suggests that these programs and other efforts to restore and support populations of bobwhites should be cognizant of the potential role of landscape context in determining the success of the effort. That is, restoration efforts are most likely to be successful in landscapes that provide an adequate proportion of favorable land cover types such as cropland, pastureland, and rangeland. Obviously, redesigning entire landscapes for the sole purpose of restoring and preserving bobwhite populations is not feasible. However, private landowners, public land managers, and quail biologists might be able to complete general and rapid assessments of current landscapes, using geographic information systems technology and photo-interpretation, to evaluate the potential success of a planned restoration effort or to select areas most likely to lead to success.

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Appendix: Randomization Test for Finding Significantly Increasing and Decreasing Bobwhite Populations

I implemented the randomization test in the following way:

1. I determined the population trend for the real data (m_{real}) as the slope of the linear least squares regression line of abundance versus year.
2. I randomized the order of the abundance data for each observer only within the observer. (For example, assume observer 1 recorded 30, 27, 20, 21, and 18 bobwhite individuals in the years 1966–1970. Upon randomization these data might become 21, 30, 18, 27, and 20 or some other order.) In this way, I randomized the data recorded by every observer.

3. I obtained the population trend (m_{rand}) for the randomized data produced in step 2 as the least squares regression line.
4. I repeated steps 2 and 3 a specified number of times (1,000), so as to produce a statistical distribution of m_{rand} values.
5. I assessed the statistical significance of m_{real} by comparing it to the distribution of m_{rand}. When m_{real} was positive, the proportion of m_{rand} values greater than m_{real} was determined. When m_{real} was negative, the proportion of m_{rand} values less than m_{real} was determined. Proportions obtained in this way can be interpreted as P values. (For example, if $m_{real} = 1.30$ and only 2 of 1,000 m_{rand} values are greater than m_{real}, then $P = 0.002$, and we conclude that m_{real} is significantly large and thus the bobwhite population exhibits a significant increase.)

Note: The null hypothesis for the randomization test was that m_{real} was due solely to the observer effect (i.e., differences among observers in their accuracy of counting birds). The randomized data (m_{rand} values) retain the observer effect because only the order of the data within an observer is randomized, not the order of the observers. Thus, if m_{real} is significant, it is because there is a real population trend in the observed data in addition to a possible observer effect. Time-series data are also temporally autocorrelated; however, this does not preclude the use of regression for obtaining the slopes (m_{real} and m_{rand}). The quantity m_{real} is used only as a test statistic to detect a significantly positive or negative trend (when compared to the distribution of the m_{rand} values) and not to test whether there is a significant fit of the regression line to the observed data.

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