PART I

INTRODUCTION

CHAPTER ONE[1]

INTRODUCTION

We shall not cease from our exploration
and the end of all our exploring
will be to arrive where we started
and know the place for the first time.
T. S. Eliot

Preventing continued decline of at-risk populations requires an intimate knowledge of the population dynamics of a species, including the intrinsic and extrinsic factors influencing those dynamics. A process that has proven useful in reaching this level of intimate knowledge is modeling of the transient ebbs and flows in population abundance. This modeling is usually conducted with incomplete knowledge regarding the biology of a species, but is nevertheless used to infer behavior of mechanisms influencing their population dynamics. Recently, aspects of a spatial nature have come to dominate the discourse on population dynamics (Harrison 1994, Hanski 1999).

Wildlife population abundance varies over space and time, and factors influencing these variations over time do not necessarily act equally over space. To simplify analyses, initial ecological investigations into the temporal fluctuations in population abundance were resolved at the expense of problems in abundance over space.

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[1] This document has been formatted largely following guidelines for the Journal of Wildlife Management.

Population size was usually modeled as a time series of Births, Deaths, Immigrations, and Emigrations, the familiar BIDE equations (Gotelli 1995). Understanding how populations vary in each of these factors is critical for predicting their persistance (Curnutt et al. 1996, Ranta et al. 1998). Populations with highly variable abundance, for instance, are more likely to become extirpated than less variable populations (Pimm 1993).

Often, early population models instituted some fairly strict assumptions, one of which was that populations were assumed closed to immigration. Thus, change in abundance was often modeled simply as a function of births minus deaths (B - D). While the assumption of a closed population was mathematically convenient, leading to the development of, for instance, the logistic growth model, it was not biologically reasonable. As Gotelli (1995:90) suggested, animal movement is the "dominant cause of population change" for some animals (e.g., migratory salmon) and thus immigration and emigration cannot always be ignored.

To account for movement of individuals as a source of population change, Levins (1970) developed the metapopulation concept. A metapopulation is a population of populations whose persistence is intimately tied to a dynamic balance between persistence of local populations, immigration from neighboring populations, and egress of dispersers to surrounding suitable habitat. The concept of metapopulations changed the focus of population demographic studies from investigations of abundance into studies of population persistence and spatial structure. For instance, spatially-structured populations form either "patchy populations" existing in complete isolation from each other (Harrison 1994, Hanski et al. 1995), as a mainland-island situation where ≥1 large population(s) is surrounded by smaller populations dependent on immigrants from the mainland for continued persistence (Hanski and Gyllenberg 1993), or as some intermediate combination of these 2 extremes. Wells and Richmond (1995:461) provided the following criteria to distinguish the 2 modalities:

> "If individuals breed in >1 spatially disjunct group during a breeding season, the groups should be considered a single population spread over a patchy habitat. If individuals breed within a single spatially disjunct group during a breeding season, but some breed in a different spatially disjunct group in another breeding season, the groups should be considered a set of populations making up a metapopulation."

The classical equilibrium paradigm suggested a negligible influence or interaction of historical effects, spatial heterogeneity, stochastic factors, and occasional environmental perturbations on the governance of population dynamics (Wu and Loucks 1995). Under this rationale, ecologists were safe separating studies of populations in space from those over time. Most early examinations of space were assumed static, ignoring temporal inertia of, or constraints in, population dynamics (Morrison et al. 1992). However, it is increasingly clear that temporal and spatial variability in abundance are explicitly related. Processes generating specific patterns of temporal variability necessarily generate characteristic patterns in spatial distribution (Sauer and Droege 1990, Curnutt et al. 1996). This interaction of space and time and their joint products have recently captivated interests of population ecologists (e.g., Waller et al. 1997, Lucas et al. 1998).

Spatio-temporal modeling is increasingly common in disciplines outside of ecology (e.g., agriculture, Bakhsh et al. 2000; epidemiology, Sanson et al. 1991, Carrat and Valleron 1992, Filipe and Gibson 1998; real estate, Pace et al. 1998). Biogeographers have long recognized the limitation of population distributions by multiple environmental factors (Shelford 1911, Udvardy 1969); that these limitations in population distribution operate over multiple spatial and temporal scales is increasingly evident (Levin 1992, Bevers and Flather 1999). There is a growing need, however, for statistical descriptions of population fluctuations in both space and time (Cuperus and de Bruyn 1987).

There are 2 distinct approaches to modeling problems in space-time, the *conjoint* method and the *prioritizing* method. The conjoint approach involves modeling the interaction of space and time explicitly; this approach is mathematically intensive and often untractable for messy ecological data. The prioritizing approach, also called the hierarchical approach, involves modeling 1 dimension and then making the parameters of the other dimension depend on the coordinates of the first dimension. For instance, time series can be modeled at each point in space so that time-series parameters are spatially-specific. Conversely, spatial models can be modeled at different points in time so that the spatial parameters are time-specific. Because there are currently no flexible families of conjoint models, most analyses of the space-time problem are hierarchical. Thus, they tend to suffer from a cohesive integration of the space-time problem.

My aim in this dissertation is to describe temporal and spatial patterns in Northern Bobwhite distribution and abundance in Illinois and where possible elucidate connections between these patterns. This approach, by all intents and purposes, is hierarchical, in that insights into species dynamics are considered within separate spatial and temporal domains. Interaction is largely implied.

PROBLEM STATEMENT

Of the ~236 species of Galliformes, 27% are threatened with global extinction compared to 11% for birds as a whole (Rands 1992). Moreover, up to ⅔ of the non-threatened galliform species are declining in abundance and/or range (McGowan et al. 1994).

One of these galliforms, the Northern Bobwhite (*Colinus virginianus*, hereafter bobwhite) has also declined in abundance across its geographic range (Brennan 1991). Analyses of North American Breeding Bird Survey (NABBS; Droege and Sauer 1990, Church et al. 1993) and Christmas Bird Count (CBC; Brennan 1991) data indicated bobwhite have declined in 77% of the states in their range since the late-1960s. Published NABBS estimates indicated bobwhite abundance in North America declined by 2.3% $\cdot$ yr^{-1} between 1966 and 1993 (Peterjohn et al. 1994). Recent estimates from the NABBS home page indicated the decline was 2.8% $\cdot$ yr^{-1} ($P < 0.01$) since 1966 and 3.7% $\cdot$ yr^{-1} ($P < 0.01$) since 1980 (Sauer et al. 2000).

In Illinois, the annual decline between 1966 and 1988 was 5.3% $\cdot$ yr^{-1} (Fig. 1.1; Droege and Sauer 1990). The decrease in Illinois was greatest between 1966 and 1979, with an estimated annual decline of 6.5% $\cdot$ yr^{-1} ($P < 0.01$). Recent analyses by Sauer et al. (2000) indicated a trivial decline in Illinois of 1.1% $\cdot$ yr^{-1} ($P = 0.14$) since 1980.

Current hypotheses suggest declines in abundance may reflect long-term alteration of habitat at both the site- and landscape-level (Klimstra 1982, Sorrow and

Webb 1982, Brennan 1991, Roseberry and Sudkamp 1998, Brennan et al. 2000). Therefore, a hierarchical approach integrating information across several spatial scales may be

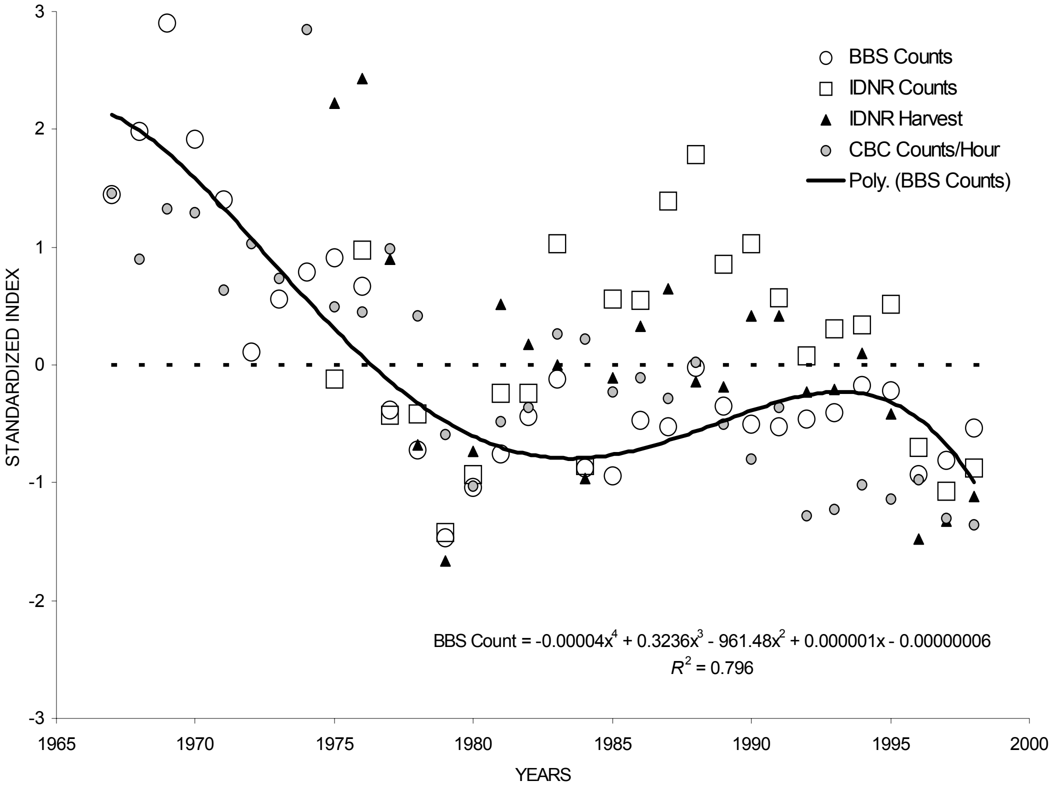

Figure 1.1. Annual North American Breeding Bird Survey (BBS) and Illinois Department of Natural Resources (IDNR) Bobwhite call counts, harvest in Illinois, and Christmas Bird Counts (CBC)/Hour from 1967 to 1998. A higher-order polynomial was

fitted to the BBS data to demonstrate the general trend in the time series.

necessary in bobwhite management to prevent further declines in abundance (Roseberry and Sudkamp 1998). For instance, Roseberry and Sudkamp (1998) proposed enhancement of sites within suitable bobwhite landscape-level habitat as a more worthy endeavor than improving habitat in ephemerally occupied landscapes. Without due consideration for the interaction of site- and landscape-level requirements of bobwhite, site-level management actions developed for 1 type of landscape may adversely influence bobwhite populations when instituted in another, much different, landscape. Bobwhite existing in ample, contiguous patches of mediocre site-level habitat, for instance, may benefit from different management strategies than bobwhite occupying isolated patches of optimal habitat. One situation would require enhancement of site-level conditions while the other situation may benefit from increased connectivity to neighboring habitat.

OBJECTIVES

Despite being one of the most studied vertebrates, little information exists regarding landscape-level influences on Northern Bobwhite population dynamics. Furthermore, virtually no information exists regarding the dynamics of bobwhite abundance over both space and time. Understanding temporal and spatial variability in bobwhite populations is essential to understand mechanisms regulating their distribution, abundance, and persistence. Therefore, objectives of this study were to 1) estimate historical temporal and spatial patterns in bobwhite population dynamics and determine their contribution to current dynamics; 2) estimate bobwhite population distribution and abundance in Illinois, primarily because successful population management dictates a clear understanding of where and at which abundance levels populations currently exist; 3) determine the structure of current populations, i.e., whether these populations exist in isolation, as a metapopulation, or, potentially as a series of semi-independent networks of metapopulations; and, finally, since the structure of populations is also important in whether they persist into future generations, 4) determine environmental and historical factors at multiple spatial scales contributing to their distribution, abundance, and persistence.

THE SPECIES

Biology and Ecology

The Northern Bobwhite is a small (140-225 gm, 25 cm tall) mottled-gray, brown, black, and white galliform, widely distributed across the eastern US. The species is sexually dichromatic; males are easily distinguished from females by their white throat and supercilium, and when alerted, a slightly raised head-crest (Ehrlich et al. 1988, Brennan 1999). Cryptically colored, Chapman (1916:271) suggested "[l]ike most grass-inhabiting birds whose colors harmonize with their surroundings, Bob-whites rely on this protective resemblance to escape detection" by predators.

Bobwhite are, however, short-lived, with most (~80%) surviving <1 yr (Marsden and Baskett 1958, Roseberry 1979, Lehmann 1984). Both Curtis et al. (1988) and Burger et al. (1995*a*) found as few as 5% of quail survived >1 yr, with most mortality occurring from fall to spring. Females are highly vulnerable to predation during incubation and brood-rearing, whereas males are most vulnerable during spring breeding displays. Both sexes are susceptible to extremes in winter weather (see references in Chapter 6).

The primary evolutionary response to this low annual survival (as well as periodic catastrophic declines) is a highly flexible and productive mating system (Burger et al. 1995*b*). Male bobwhite in Illinois begin calling the familiar 2- or 3-note whistle call ("bob-white") in early April and continue calling into August, signaling the period of reproduction. The majority of females are polyandrous; the female often may lay 1 clutch for incubation by a male and then lay another clutch which she incubates (Emlen and Oring 1977, Burger et al. 1995*b*). Males incubate up to ⅓ of all nests (Stoddard 1931, Klimstra and Roseberry 1975, Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995*b*). Bobwhite incubate 12–16 egg clutches, and are capable of up to 3 nesting attempts per season (Curtis et al. 1993, Burger et al. 1995*b*, Guthery and Kuvlesky 1998). Such a reproductive strategy allows bobwhite populations to increase in abundance by as much as 400% per year (Roseberry and Klimstra 1984).

Burger et al. (1995*b*:425) suggested the bobwhite mating system "might be an adaptation to the fluctuating resources characteristic of ephemeral, disturbed habitats," which are favored by bobwhite. Bobwhite occur in early successional habitats across a wide variety of vegetation types (Rosene 1969, Lehmann 1984, Roseberry and Klimstra 1984). However, occupied habitats must meet very specific requirements during nesting and brood-rearing periods. Nests are constructed from dead, fine-stemmed grasses situated beneath live clumps of perennial cover, and are typically located in "scattered shrubs and briars interspersed with a moderately dense stand of herbaceous and grassy vegetation" (Klimstra and Roseberry 1975:17). The majority of nests are placed ≤ 5 m from a "noticeable break in cover pattern" (Klimstra and Roseberry 1975:17) and typically occur at a density of 14–16 $\cdot 100\ \text{ha}^{-1}$ of good habitat (Roseberry and Klimstra 1984). Prime brood-rearing habitat is characterized by openness at ground level, overhead cover to protect from aerial predators, and sufficient forage of annual weeds, legumes, and insects (Hurst 1972). Bare ground or sparse litter allow bobwhite ease of movement, access to seeds (Schroeder 1985), and areas for dusting (Rosene 1969).

In Illinois, bobwhite in all seasons favor agricultural fields, old fields, pastures and other grasslands, and forests (Roseberry and Klimstra 1984, Brennan 1999). Roseberry and Sudkamp (1998) found optimal conditions for bobwhite occurred in a diverse, patchy landscape containing abundant woody edge and moderate amounts of grassland and row crops. In high-quality habitat, fall-early winter densities typically range between 2.2 and 4.4 birds $\cdot\ \text{ha}^{-1}$, depending on the successional state of the vegetation type (Brennan 1999).

Bobwhite are largely sedentary within these successional habitats, moving primarily from 2-yr post-successional vegetation preferred for nesting to 1-yr post-successional habitats favored for brood-rearing and general foraging (Brennan 1999). Most annual movements are between 0.8 and 1.6 km (less than the width of 3 home ranges), therefore, habitats of varying successional states must be available within close proximity. It is this juxtaposition of habitat, along with the age and reproductive status of the individual, that influences home range size and location (Brennan 1999).

Notes on the Status in Illinois

Historically, bobwhite were probably most abundant in the mid-19th century (1846-1854), when human settlement converted 10–20% of the landscape into agriculture, yielding an ideal combination of food and cover (Kabat and Thompson 1963). Thereafter, bobwhite abundance declined. Kabat and Thompson (1963) suggested that a decline in bobwhite abundance in Wisconsin from 1937–1962 was directly correlated to the loss of hedgerow cover. Why bobwhite declined between 1854 and 1937 was not mentioned by Kabat and Thompson (1963), but I suggest it may be due, in part, to overhunting; it is well-established that the loss of Wild Turkeys (*Meleagris gallopavo*) and white-tailed deer (*Odocoileus virginianus*) from much of the eastern US during this period was due to overharvest (McCabe and McCabe 1984, Kennamer et al. 1992), and similar forces were likely acting on bobwhite.

Preno and Labisky (1971) and Edwards (1972) suggested bobwhite may have reached a recent apex in abundance in 1969. Others would argue quail numbers were equally high throughout the 1950s and 1960s (J. L. Roseberry, personal communication). Preno and Labisky (1971) suggested bobwhite reached late winter (pre-breeding season) densities of 0.2 birds $\cdot$ ha^{-1} in 1969. Bobwhite harvest has declined dramatically in recent years, as approximately 2.85 million bobwhite were harvested in 1958 and 2.39 million in 1969, but only 0.40 million in 1979 and 0.54 million in 1998. Currently, bobwhite occupy every county in the state and are most abundant in the westcentral and southern portions where agricultural and forested lands are interspersed.

THE STUDY LOCATION

The research population for this study included all bobwhite and potential habitat of bobwhite in Illinois, an important agricultural state in the midwestern US. Much of the topography and land cover in Illinois reflects glaciation events of the Pleistocene (Willman and Frye 1970, Fehrenbacher et al. 1984). The Illinoian glaciation (300,000-125,000 YA) overlaid ~80% of the state, whereas the subsequent Wisconsinan glaciation (75,000-10,000 YA) covered ~45%, largely in the area of the corn till plain of east-central Illinois. The product of these glacial events was a relatively flat topography ($\bar{x}_{slope} = 0.6°$) and a rich soil base described as one of the most productive in the world (Fehrenbacher et al. 1984). The predominant soils, occupying ~63% of the state, developed largely from loess.

Areas untouched by glaciation, the Shawnee Hills in the south and the Wisconsin Driftless Section in the extreme northwest, exhibit greater topographical relief. In between, the state is bisected by weak moraines, the Illinois, Kaskaskia, and Rock Rivers, and their tributaries[2]. The Mississippi River bounds the west side of the state, the Ohio River the south, the Wabash River the southeast, and Lake Michigan the northeast, effectively isolating Illinois on 77% of its perimeter.

Climate is temperate, with mean annual temperature ranging from 8–15° C (from north to south, respectively). January is typically the coldest month, with mean temperature ranging from -6–2° C. Mean temperature in July (usually the hottest month)

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[2] Willman and Frye (1970:27) suggested the Illinoian glaciation left the resulting till plain “distinguished by a flatness scarcely equalled by most lake plains.”

ranges from 23–27° C. Mean annual precipitation ranges from 13–18 cm.

A dry, warming period which persists to this day began in Illinois approximately 4,000–6,000 YA, leading to expansion of grassland in central and northern Illinois and retreat of forests into stream valleys. This is most likely when bobwhite colonized Illinois, moving in from the south. Subsequent anthropogenic influences have led to the modification of land cover so that today Illinois consists chiefly of row crops such as corn and soybean (54%) and grainfields (6%), with lesser elements of grassland (19%) and woodlands (11%; Illinois Department of Natural Resources 1996). The Natural Resource Conservation Service estimated a 1.5% decrease in total rural land from 1982 to 1997, roughly 13,000 ha · yr^{-1}. This decline was most evident in pasture grasslands, which declined by 22%.

THE DATA SETS

Two indices of relative bobwhite abundance were used in this study: North American Breeding Bird Surveys (count/stop and mean and total count/route), and Illinois Department of Natural Resources (IDNR) Northern Bobwhite Call Count Surveys (number of males/stop and number of males/route; 1974–1998). Wildlife managers have used roadside counts of whistling bobwhites as an estimate of relative abundance for >50 yrs (Bennitt 1951, Elder 1956, Rosene 1957, Norton et al. 1961). The count indices indicate relative rather than absolute abundance (Baxter and Wolfe 1973), with the assumption that the indices are directly proportional to population size (Skalski and Robson 1992; however, see Burnham 1981, Boonstra 1985, and Nichols 1986 for criticisms of the use of simple counts as indices of abundance). The proportionality constant dictating the relationship between relative abundance and absolute abundance is the species-specific probability of detection. Unfortunately for bobwhite, this proportionality constant is unknown.

The NABBS[3], annually administered in June by the U.S. Fish and Wildlife Service, consisted of 81 39.4-km routes along secondary roads in Illinois (Fig. 1.2). Each route possessed 50 evenly spaced stops at which skilled volunteer observers counted all bobwhite (in addition to other bird species) seen within a distance of 400-m and all heard at any distance during 3-min intervals (Droege 1990). Surveys began 0.5-hr before official sunrise and were conducted only during acceptable weather (good visibility and little or no precipitation or wind). Dependent young in bobwhite broods were not counted when seen. Counts were collected from 1966–1998 (n = 87,200 stop counts). Data collected prior to 1998 were manually entered for each stop from microfiche of data sheets. Stop-specific count data for 1998 were transferred from the NABBS home page (USGS Patuxent Wildlife Research Center 1999) and incorporated into the data set. Greater detail for the NABBS methodology is provided by Robbins et al. (1986).

The IDNR Northern Bobwhite Call Count Surveys conducted each year in June consisted of 53 32-km routes along secondary roads in Illinois (Fig. 1.2). Each IDNR route possessed 20 evenly spaced stops at which IDNR personnel counted all bobwhites

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[3] Both the NABBS and IDNR bobwhite call counts and their associated UTM coordinates are electronically archived at Southern Illinois University at Carbondale’s Cooperative Wildlife Research Laboratory. The survey locations for the IDNR pheasant call counts, which were used for validation, are also available in this archive.

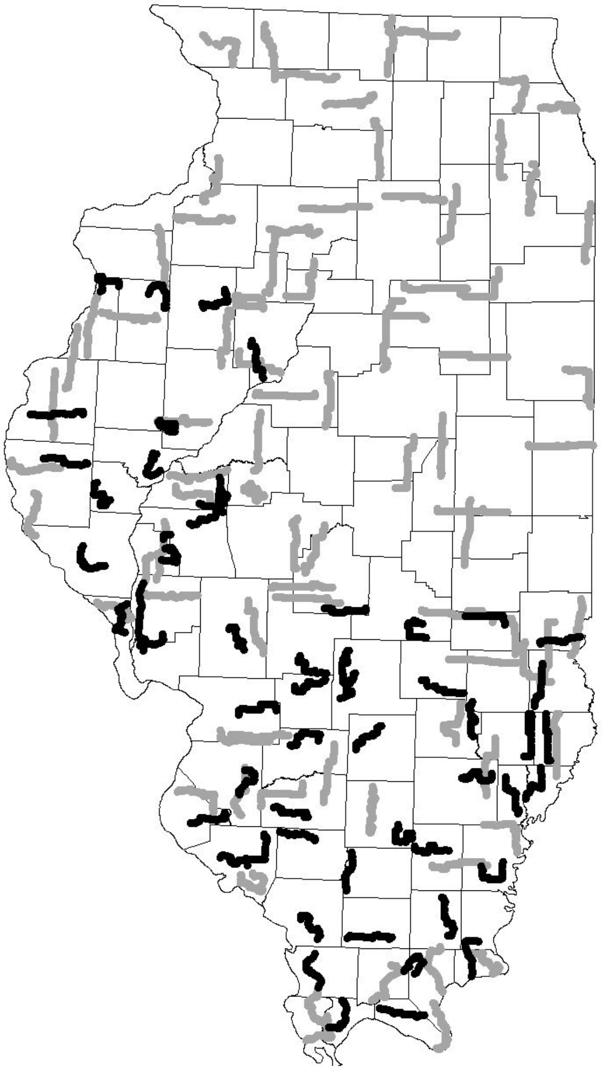


Figure 1.2. Distribution of North American Breeding Bird Survey (in gray) and Illinois Department of Natural Resources Bobwhite Call Count Survey (in black) locations in Illinois.

seen or heard in a 2-min period. Routes were run once per year from 5–25 June (Illinois Department of Conservation-Division of Wildlife Resources 1994). These routes were tailored to occur at daily and seasonal peak calling.

Georeferencing

All stops on both NABBS and IDNR routes were digitized (Cooperative Wildlife Research Laboratory, Quarterly Progress Report, W-106-R, April-June, 1999). All IDNR routes were digitized from hard-copy maps. Forty NABBS routes were sufficiently documented on hard-copy maps to provide reasonably accurate coordinates for NABBS stops; stop locations on 6 routes were determined with the aid of more detailed maps provided by V. Kleen (Illinois Department of Natural Resources). For the remaining 35 routes, individual NABBS survey volunteers (*n* = 27) were mailed topographic maps for routes they had run in past years. More than 120 digital raster graphs were downloaded from the Illinois Natural Resources Geospatial Data Clearinghouse (http://www.isgs.uiuc.edu/nsdihome/webdocs/st-geolo.html/) to create the topographic maps covering the area of the NABBS routes. The maps were sent to observers to coincide with the approximate time period (May to June) in which NABBS routes are annually run in Illinois. Each observer was asked to mark and number specific stop locations on provided topographic maps, and then return the edited maps in an accompanying self-addressed stamp envelope to the Cooperative Wildlife Research Laboratory.

Spatial accuracy of NABBS routes was verified by 2 methods. The aforementioned mailing was used to obtain verification by 8 observers for the stop locations for routes previously entered into the geographic information system (GIS). I also retrieved an ArcView (Environmental Systems Research Institute, Redlands, California, USA) shapefile of the Breeding Bird Survey Routes of North America from the National Atlas of the United States website (http://www.nationalatlas.gov/birdm.html). This digital coverage contained the active NABBS routes for the lower 48 States. This includes many new routes added in 1998, though not all of them; the discontinued routes were generally not digitized.

I reprojected the shapefile from Lambert to Universal Transverse Mercator, and from North American Datum (NAD) 1983 to NAD 1927. The Illinois routes were selected from the data set and converted into an Illinois-only data set. This data set was then compared qualitatively to the NABBS stops that were previously digitized (Cooperative Wildlife Research Laboratory, Quarterly Progress Report, W-106-R, April-June, 1999).

Overall, the 2 data sets coincided quite well. Some of the reasons for differences between the 2 data sets are suggested by the Metadata for the Breeding Bird Survey Routes of North America. If the NABBS route did not start at an intersection, the starting point for the National Atlas-digitized route may have been slightly off. Portions of the NABBS route were sometimes skipped because of traffic noise or overlap with other routes; these skipped portions were usually not indicated. The maps National Atlas used did not always indicate the exact ending points of the routes, so in many cases the ending points were estimated and the digitized routes were longer or shorter than the actual route. Occasionally portions of the roads on which surveys were conducted were not contained on the digital road files used by National Atlas; in these cases the road locations were very roughly estimated. I also found routes may have shifted somewhat through observer discretion; in informal discussions with Illinois NABBS surveyors this did not seem to be a large source of error, but it is an error accommodated by neither data set. For the above listed reasons, I believe the geographic data set I am using, stops digitized by the Cooperative Wildlife Research Lab, is a more accurate reflection of where bobwhite (and other birds) were actually seen and heard.

Comparability of Abundance Indices

The data sets are consistent with each other. Ignoring serial correlation, which inflates the strength of the relation, the Pearson correlation coefficient between the NABBS and IDNR call count data was 0.527 for the years 1974–1998 ($\rho_{\mathrm{NABBS:IDNR}} = 0.527$, $P < 0.01$). The relationship between spring IDNR call counts and fall harvest, another index of regional abundance, was similar ($\rho_{\mathrm{IDNR:HARV}} = 0.525$, $P < 0.01$). However, the better predictor of fall harvest was the NABBS data set ($\rho_{\mathrm{NABBS:HARV}} = 0.810$, $P < 0.001$). Of the 2 call count surveys, the IDNR survey was more consistent in the area surveyed each year (Fig. 1.3), with each survey typically covering approximately 450 $\mathrm{km}^2 \cdot \mathrm{yr}^{-1}$.

To assess the agreement between NABBS and IDNR call counts, I examined IDNR and NABBS stops <420 m of one another. The mean difference in count between the 2 data sets was 8.45 and the correlation was low ($\rho_{\mathrm{NABBS:IDNR}} = 0.199$, $P \approx 0.2$). Some

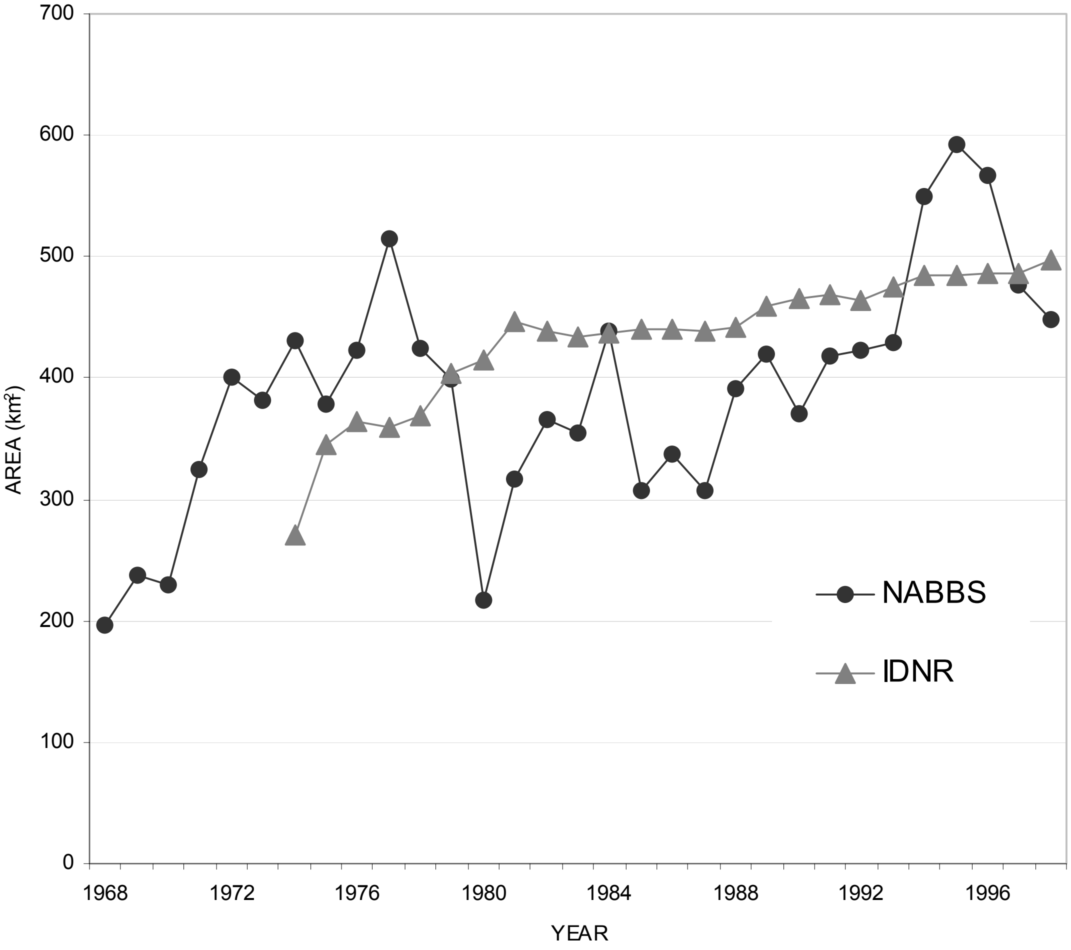


Figure 1.3. Annual area surveyed by Illinois Department of Natural Resources (IDNR) Bobwhite Call Count and North American Breeding Bird Surveys (NABBS) in Illinois.

of this difference between the 2 data sets must be related to the following:

1) IDNR surveyors were listening only for bobwhite, whereas NABBS surveyors were listening for all birds,

2) IDNR routes were run specifically when bobwhite were most likely to call, whereas NABBS routes may have been run too early or too late for maximal effectiveness, and,

3) IDNR routes were run at the point in the season when calling was at a maximum. The NABBS routes were run any time during the spring.

Casual inspection of the distribution of the stops suggested a large portion of the counts occurred too early and too late in the morning, coincident with the second reason. Additional differences may have been due to weather, though both should be run under ideal climatological conditions for listening.

Assumptions About the Data

Annual observations were assumed taken under roughly identical conditions, i.e., no overly undue influence of weather or observer experience, for instance. The 2- or 3-note whistle call made in early spring by the male bobwhite is readily distinguishable, even to novice birders. As such, there should be little error in identification by observers for this species, and thus less potential for observer bias (Sauer et al. 1994) or sampling-induced count stochasticity (Barker and Sauer 1992). However, NABBS routes may cover periods of the morning when bobwhite are less apt to call. Surveys 20 min before sunrise and 2 hrs after sunrise possess the greatest chance of missing bobwhite (Robel et al. 1969, Wilson and Guthery 1999). The IDNR routes are less affected by this bias because they are designed to occur specifically when bobwhite call.

Validity of Indices as Measures of Abundance

Gaston and McArdle (1994) suggested indices of abundance for open populations with no recognizable natural boundary cannot be used to measure population size itself, but rather are indices of population density. Indices of abundance and measures of trend and variability in these indices were estimated for sites and routes. While the indices used in this study are density measures, I will often refer to these measures as describing a population.

Burnham (1981) warned of using unvalidated count indices. The proper means of validating an index is to calibrate the index with a census having limited or known bias (e.g., mark-recapture). Unfortunately, the NABBS has not been validated in this manner (S. Droege, personal communication). Fortunately, however, Dimmick et al. (1982) and DeMaso et al. (1992) provided surrogate measures of validation for bobwhite, suggesting coveys heard was linearly related to covey density (see Roseberry and Klimstra 1984:103 for a review of the subject). The conclusion is that number of calling males is likely linearly related to bobwhite density.

One additional difficulty with using count data as indices to abundance is the ratio of within-site variability to between-site variability. If within-site variability is relatively high, examining differences between sites is not useful. Link et al. (1994:1102) found Northern Bobwhite counts as conducted by NABBS were highly repeatable within-site.

Approximately 15% of the variance in bobwhite counts was due to within-site differences; this means 85% of the variation was due to among-site differences. Link et al. (1994) also reported no within-site differences due to season, indicating that counts were highly similar when conducted during any part of the annual NABBS survey.

Validation Data

Christmas Bird Count (CBC; Bock and Root 1981, Butcher et al. 1990; http://www.mp1-pwrc.usgs.gov/birds/cbc.html) and IDNR pheasant call counts were examined to validate models (Fig. 1.4). Both CBC and pheasant call counts note the presence of bobwhite. The CBC is collected state-wide, but is biased around urban areas in northern and central Illinois. The IDNR pheasant call counts are conducted outside of the historical quail range in northern and eastern Illinois. Within the historical quail range, validation also occurred with IDNR bobwhite call count data.

Scale

To examine whether a hierarchical approach is necessary for a successful understanding of bobwhite autecology, relationships between habitat and bobwhite abundance and distribution were evaluated at multiple spatial scales (Appendix 1). Scale-related differences were examined by varying spatial extent; thus, NABBS and IDNR survey locations were buffered by 126, 400, 1,260, and 4,000 m (n = 4,104 and 1,060, respectively; size range = 3–113 km^2). These 4 spatial extents are logarithmically related, as they encompass areas of 5, 50, 500, and 5,000 ha, respectively.

As spatial scale is also a function of map grain, I also varied grain. Grain is the resolution or cell size at which spatial data are relevant. For analyses involving NABBS data, I examined grains of 0.085 ha (the default grain) and 1 ha. Resolving grain size smaller was not possible given the resolution of the available imagery, and resolving a grain size larger than 1 ha seemed inappropriate given the sedentary nature of bobwhite. Because initial analyses suggested little to no change in model results due to variation in spatial grain, and for the sake of brevity, I have not included those results here.

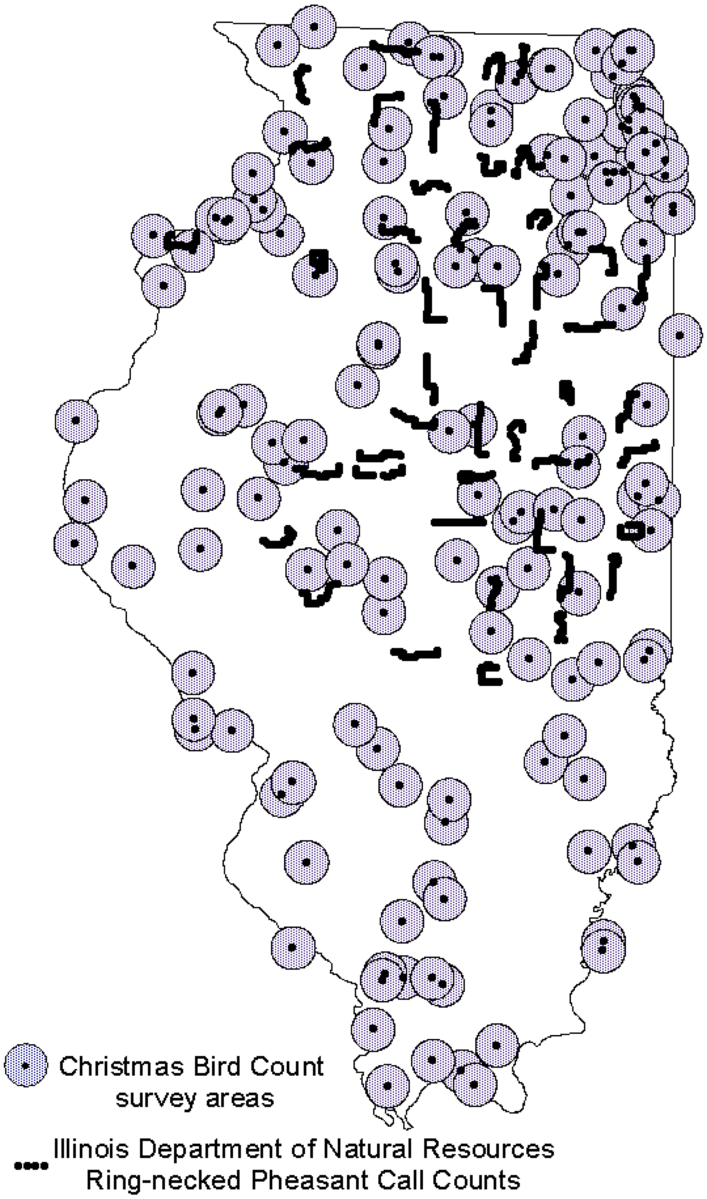
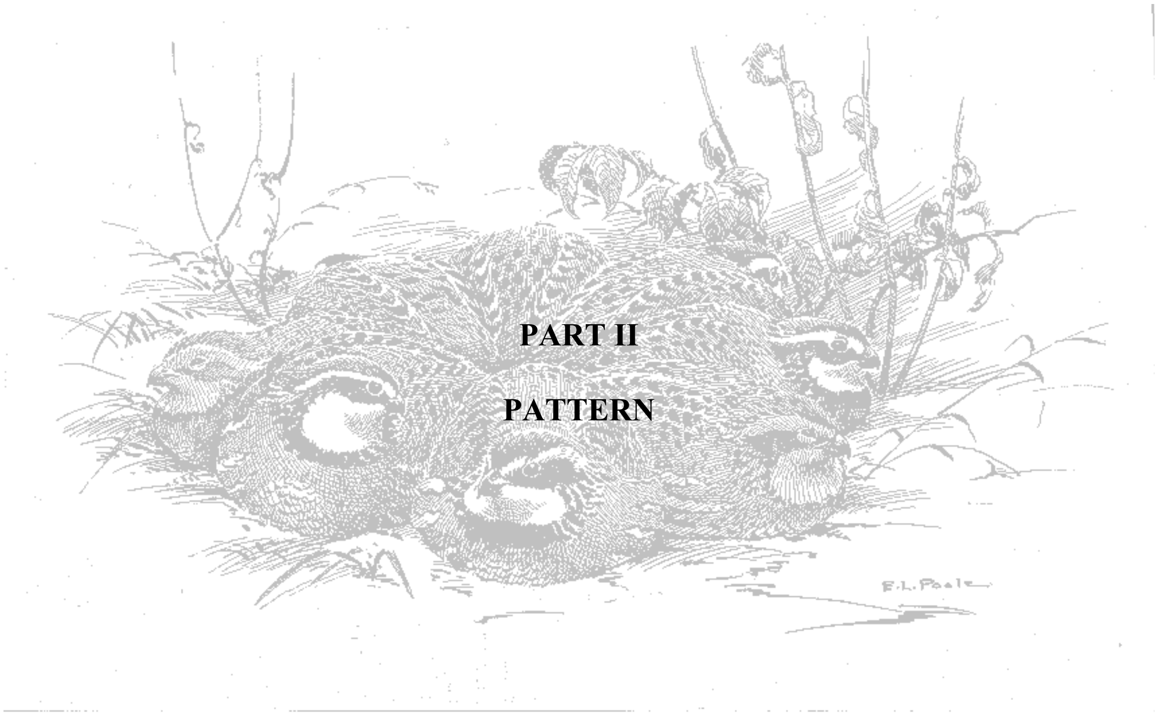


Figure 1.4. Distribution of Christmas Bird Count locations (with 12.1 km buffer delineating survey area) and Illinois Department of Natural Resources Ring-necked Pheasant call counts in Illinois, 2 independent data sets used to validate spatially-explicit models of Northern Bobwhite habitat.

PART II

PATTERN



CHAPTER TWO

HISTORICAL PATTERNS IN POPULATION DYNAMICS OF NORTHERN BOBWHITE IN ILLINOIS: A 32-YEAR RETROSPECTIVE ANALYSIS

I do not know which makes a man more conservative -
to know nothing, but the present, or nothing, but the past.
John Maynard Keynes

Critical acumen is exerted in vain to uncover the past;
the past cannot be presented...
it is the province of the historian to find out, not what was,
but what is.
Henry David Thoreau

To know where we are going, it is often important to know where we have been, and where we are at present. The purpose of this chapter is to briefly summarize and describe historical patterns in bobwhite abundance in Illinois. Long-term trends and historical effects have a disproportionate effect on variability in animal population parameters (Pimm and Redfearn 1988). However, few long-term studies of wildlife species (Likens 1989, Leopold and Hurst 1993, Leopold et al. 1996) exist to be able to estimate extent of this natural variability. Pelton and van Manen (1993) found ~80% of studies published in the *Journal of Wildlife Management* from 1980–1995 were ≤5 yrs, whereas 68% of studies in *Wildlife Monographs* were ≤6 yrs. None of the studies in either review included Northern Bobwhite, a deficiency in the research history of the bobwhite that Robel (1993) called for fulfillment.

Programs monitoring species abundance are plentiful, especially for birds.

Long-term monitoring schemes such as the NABBS (Robbins et al. 1986), CBC (Bock and Root 1981), British Common Bird Census (Furness and Greenwood 1993), and Finnish land bird monitoring scheme (Koskimies and Väisänen 1991), provide comprehensive, ongoing databases of avian abundance covering several decades. Many other local studies provide databases covering ≥10 years (Hogstad 1993), including bobwhite. Errington's (1957) study in Wisconsin lasted >25 yrs, whereas Aldo Leopold carried out various studies over a 15 yr period beginning in the late 1920s (Leopold 1933). Research activities of Roseberry and Klimstra (1984) in Illinois extended >15 yrs and analysis of hunter-submitted bobwhite wings has occurred continuously in Illinois since 1950.

Pelton and van Manen (1993) suggested 4 ecological phenomena deserved long-term study, 1) slow processes, 2) rare processes, 3) processes with high variability, and 4) subtle and complex processes. This chapter addresses the third phenomena; bobwhite populations are notoriously variable. Short-term field studies and analyses of monitoring data have suggested bobwhite are in decline across the eastern US due to various factors. The primary hypothesis for the reduction in bobwhite abundance in the eastern US has been that long-term alteration of habitat has negatively influenced the persistence of bobwhite populations (Chapter 1).

Greater than 50% of land area in Iowa, Illinois, and Indiana is in agriculture (Best et al. 2001). The 1997 Census of Agriculture (US Department of Agriculture 1998) indicated farmed area in Illinois declined from 12.1-million ha in 1964 to 11.2-million ha in 1997. Standard error of the coefficient from farm area regressed against year was small (SE = 1.00), indicating a gradual loss of ~27,000 ha annually. While farm area declined, mean size of farms gradually increased from 91 to 151 ha. Ribic et al. (1998) described increases in agricultural intensity concurrent with declines in upland wildlife habitat on Illinois farms. Coincident with these changes in agricultural area and intensity were changes in urban and suburban area as the USDA Natural Resources Conservation Service indicated developed land in Illinois increased from 7.8% of the total land surface in 1982 to 9.4% in 1997.

Given that alteration of Illinois habitat has been gradual and continuous, I hypothesize that the decline in bobwhite abundance should be gradual and continuous. The alternative hypothesis is that despite gradual habitat loss, the recent historical decline in bobwhite abundance was not gradual, and was likely due to factors other than habitat loss alone. To examine these hypotheses, I conducted a 32-yr retrospective analysis of bobwhite population dynamics in Illinois, describing historical patterns in rate of change and variation in bobwhite abundance.

This examination of alternative hypotheses is somewhat of a straw man exercise, easily knocked aside by inspection of a simple time series of bobwhite harvest (Fig. 1.1). This exercise is necessary, however, to justify various approaches I take in later chapters as it will become evident that considerable variation in historical abundance cannot be explained by habitat loss alone.

METHODS

Time series of NABBS and IDNR call counts and IDNR harvest were related to a time series of Illinois farm area with Pearson moment correlation. Total land in Illinois annually devoted to agriculture was provided by the National Agricultural Statistics Service (http://www.usda.gov/nass); farmed land was defined as all land operated by farms during the year. It included crop and livestock acreage, wasteland, woodland, pasture, land in summer fallow, idle cropland, and land enrolled in the Conservation Reserve Program and other set-aside or commodity-acreage programs.

Descriptive statistics were calculated for NABBS and IDNR counts. The degree of decline in bobwhite abundance was assessed by fitting a least-squares regression of counts to year by the method (i.e., estimating equations) implemented by the North American Breeding Bird Survey program (Geissler and Sauer 1990, Link and Sauer 1994). The calculations were conducted online at the NABBS home page (http://www.mbr-pwrc.usgs.gov/bbs/ bbs.html). Estimating equations extract the multiplicative trend in abundance after accounting for observer variability.

Annual intrinsic rate of change (*r*) was calculated as $\ln(N_{t+1}/N_t)$. Change between a 0 count at time *t* and a count >0 at time *t*+1 was not defined. Descriptive statistics and intrinsic rate of change for the NABBS data were compared between the Pre-1980 and Post-1980 periods with the Kruskall-Wallis Rank-Sum Test. This date was chosen because examination of time-series plots (Fig. 1.1) indicated a change in population trajectory may have occurred in this year.

RESULTS

Descriptive Statistics

A total of 41,233 bobwhite was counted by NABBS surveyors from 1968–1998. Mean annual bobwhite count at NABBS survey locations was 0.51 ± 0.02. Across all years, mean counts for sites counting bobwhite was 1.55.

Based on estimating equations employed by NABBS, 47 of 59 NABBS routes exhibited negative trends for the period 1968–1998 (Table 2.1, Appendix 2.1). Median slope was -2.53 (range = -24.71–6.55).

Bobwhite counts declined by ~6.4% $\cdot$ yr^{-1} ($F_{1,12} = 12.47$, $P = 0.004$) from their apex in 1969 ($\bar{x} = 1.14 \pm 0.06$ bobwhite $\cdot$ stop^{-1}) to their nadir in 1979 ($\bar{x} = 0.22 \pm 0.01$ bobwhite $\cdot$ stop^{-1}) (Figs. 1.1, 2.1). Mean count prior to 1980 was 0.67 ± 0.03 bobwhite $\cdot$ stop^{-1}; thereafter, mean count was 0.39 ± 0.01 bobwhite $\cdot$ stop^{-1} (Wilcoxon rank-sum with normal correction; $Z = 3.61$, $P = 0.0003$). Change in mean NABBS counts between the Pre- and Post-1980 periods suggested counts for 29 of 59 (49%) BBS routes declined. Since 1981, bobwhite abundance was roughly stationary (annual change = 0.1% $\cdot$ yr^{-1}, SE of estimate = 0.3%, $F_{1,16} = 0.3$, $P = 0.59$).

A total of 264,120 bobwhite was counted by IDNR personnel from 1974 to 1998. Counts were clearly biased low in the first year of the survey (1974; $\bar{x} = 3.87 \pm 0.13$ vs. >8.33 in all other years). Excluding 1974, mean counts in the quail range varied from 8.33 to 17.83 bobwhite $\cdot$ stop^{-1}, with an across-years mean of 12.47 ± 0.39 bobwhite $\cdot$ stop^{-1}. Mean count prior to 1980 was 11.07 ± 0.18 bobwhite $\cdot$ stop^{-1}; thereafter, mean count was 12.79 ± 0.09 bobwhite $\cdot$ stop^{-1} ($Z = -1.07$, $P = 0.3$).

Table 2.1. Summary statistics for estimating equations describing temporal trends in Northern Bobwhite abundance in Illinois, 1966–1998, as derived from North American Breeding Bird Survey counts. Slope (β) is the annual percent change in abundance per year, s^2 is the variance in route abundance, and $\bar{x}$ is mean count of bobwhite on individual routes for the period 1966–1998.

Route Summary	β_1	s^2	$\bar{x}_{Count}$
median	-2.53	2.33	26.22
$\bar{x}$ (SE)	-4.02 (0.84)	3.03 (0.31)	24.06 (2.18)
minimum	-24.71	0.44	0.58
maximum	6.55	10.93	77.32

The deterministic trend in bobwhite abundance was highly associated with farmland area for 2 of 3 indices (Fig. 2.1). Greater than 50% and 30%, respectively, of the variation in NABBS and Illinois harvest trends was explained by loss of farmed land.

Intrinsic Rate of Change

Because data for individual NABBS stops were sparse (~0.5 bobwhites $\cdot$ stop^{-1} $\cdot$ yr^{-1}), intrinsic rate of change (*r*) was calculated for 10-stop increments rather than for individual stops. Mean intrinsic rate of change for bobwhite throughout Illinois for the period of study was -0.012 ± 0.009. Mean *r* for the 32-yr period was log-normally distributed (Fig. 2.2). Approximately one-third of the sample exhibited either no change in abundance (0.393) or a declining rate of change (0.312). More than one-quarter (0.290) of the sample exhibited increasing abundance.

Mean *r* for 1969–1979 (Pre-1980) indicated bobwhite abundance in Illinois was decreasing (-0.093 ± 0.018), whereas mean *r* for 1980–1998 (Post-1980) indicated bobwhite abundance was increasing (0.025 ± 0.011). A greater proportion of the sample was stationary Post-1980 than Pre-1980 (0.438 vs. 0.275); a smaller proportion exhibited high growth rates (0.012 vs. 0.015) Post-1980 than Pre-1980.

For the quail range, mean *r* was -0.351 ± 0.010. Mean *r* was bimodally distributed because of a paucity of samples with 0 *r*. Approximately half of the sample exhibited either a declining rate of change (0.562) or a low positive growth rate (0.347); 5% of the sample exhibited $r \geq 0.2$. Mean *r* in the quail range for 1976–1979 indicated bobwhite abundance decreased (-0.458 ± 0.027); unlike the state-wide estimate, mean *r* for

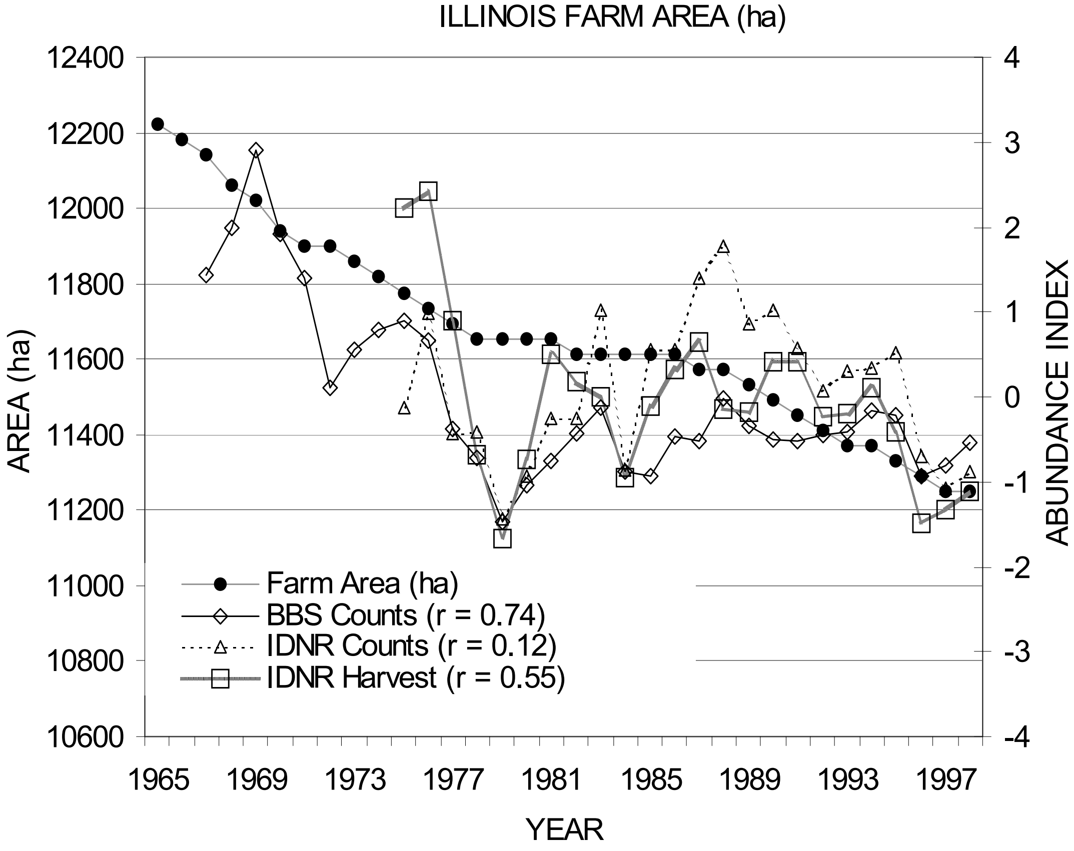


Figure 2.1. Deterministic negative trend in Northern Bobwhite abundance associated with area in Illinois devoted to farmland. Farm area was determined by the National Agricultural Statistical Service. Indices were associated with farm area with Pearson product-moment correlation.

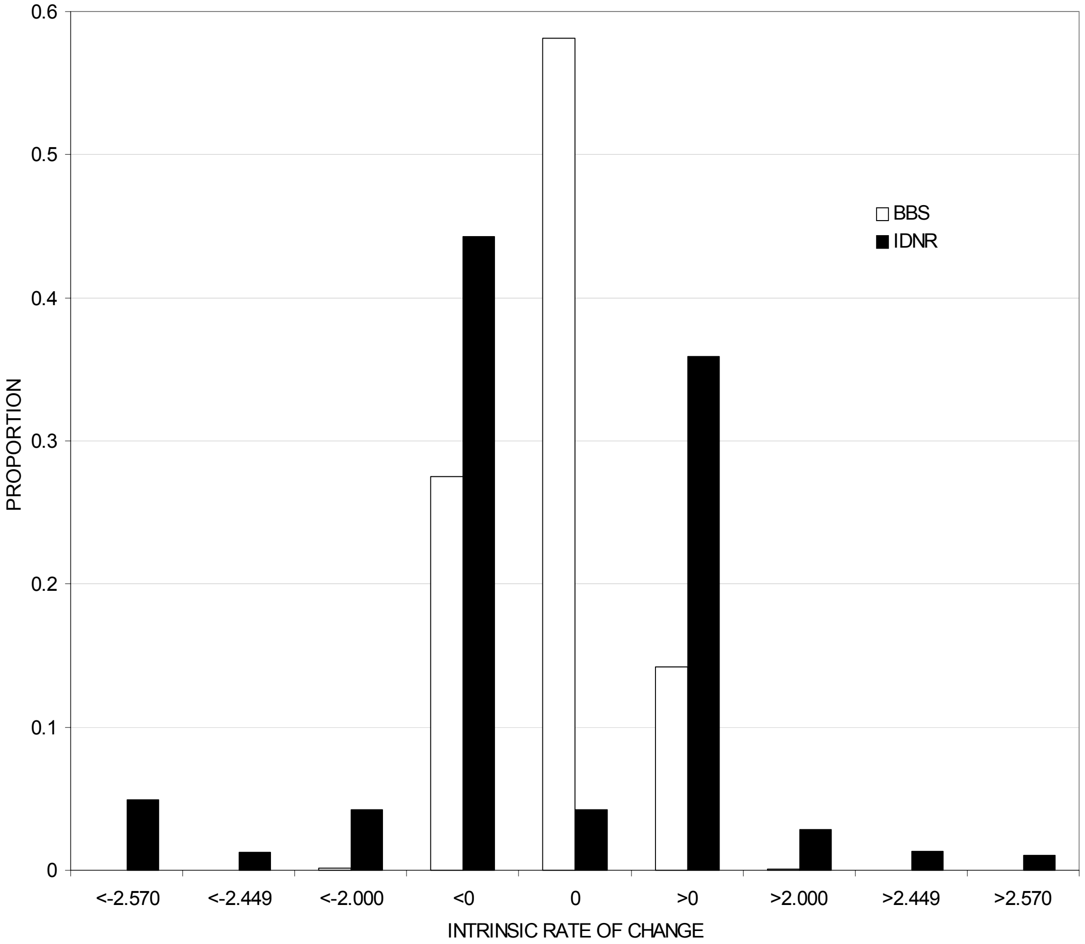


Figure 2.2. Distribution of mean rates of change (*r*) for North American Breeding Bird Survey (BBS) and Illinois Department of Natural Resources (IDNR) Northern Bobwhite route-level call counts.

1980–1998 also indicated decreasing abundance (-0.332 ± 0.011).

DISCUSSION

It is often forgotten that even species in decline may exhibit evidence of positive growth, at least in some areas and at some times (Villard and Maurer 1996). Despite a state-wide decline in bobwhite abundance over much of the period, some populations exhibited tremendous growth. More than a quarter of the survey counts exhibited a small positive r (<2), indicating an approach to carrying capacity, K, with damped oscillations (Gotelli 1995). One percent (0.01) possessed r suggestive of population dynamics exhibiting a 2-point limit cycle ($r = 2.000$–2.449), a small fraction (0.002) exhibited higher frequency limit cycles (4 or more limit cycles; $r = 2.449$–2.570), and some (<0.001) exhibited dynamics consistent with chaotic growth (nonrepeating limit cycle; $r > 2.570$).

The decline in bobwhite abundance in Illinois reflected a heterogeneity in dynamics over time with the great majority of the decline occurring from 1969 to 1979 (Chapter 3 describes this heterogeneity in decline over space). Compared to my estimated loss of $-6.4\% \cdot \text{yr}^{-1}$ between 1969 and 1979, NABBS estimated the annual decline between 1966 and 1980 as $-6.8\% \cdot \text{yr}^{-1}$ based on route regression methods (Sauer et al. 2000).

Between 1969 and 1979, bobwhite abundance declined, whereas since 1980, bobwhite abundance has been stationary, oscillating about a mean abundance. Mankin and Warner (1999) reported very similar results for the eastern cottontail (*Sylvilagus* *floridanus*) in Illinois, with cottontails declining from 1968 to 1979 and then rising to a plateau after 1981.

The eastern cottontail is an early successional species occupying many of the same habitats as the bobwhite (Ribic et al. 1998). Thus, declines associated with loss of habitat should be similar. Mankin and Warner (1999) reported an association between the change in cottontail abundance and the change in availability of pasture ($r = 0.49$), hay ($r = 0.33$), and small grain agriculture ($r = 0.27$) between the 1960s and 1980s. Each of these agricultural land use practices decreased in most of the counties (>75%) over the period they examined. They used a Classification and Regression Tree model to define the appropriate set of variables predicting cottontail decline; their final model identified pasture as the most important variable, explaining approximately 28% of the variance in cottontail decline. Presumably, the remaining 72% of variance was not explained by loss of pasture alone. The analyses of Mankin and Warner (1999) do not explain the apparent rise to a plateau in abundance exhibited by rabbits in the 1980s in the face of continued changes in land use practices. Mankin and Warner (1999) suggested that despite the continued decline in pasture, increases in the amount of woods moderated further declines in cottontail abundance.

The 2 state-wide indices of bobwhite abundance were positively correlated with farm area. These correlations are biased upward due to serial correlation within the time series; thus, the true level of correspondence between farm area and bobwhite abundance is lower. Regardless, >25% variance in abundance remains unexplained by loss of farm area.

Given that bobwhite abundance increased after 1980 to a plateau of abundance habitat loss is not likely the sole cause for the decline in observed abundance between 1969 and 1979. I suggest a large part of the remaining variance is due to historical winter weather (Chapter 6). Bobwhite have existed in Illinois for at least several millenia, and in that time severe winters must have occasionally plagued bobwhite populations, reducing their regional abundance much as they did in the late-1970s. The key difference between then and now is in the quality of habitat. If good habitat is well-connected, a thriving population should be able to rebound from a climate-related setback and re-occupy depauperate habitat, especially if the historical frequency of severe disturbances is low. However, recent loss of suitable farmland and increased urbanization of rural areas probably has fragmented favorable habitat (Chapter 8), preventing reoccupation of habitat once occupied by bobwhite.

While a more thorough treatment is warranted, similarities between historical bobwhite and cottontail abundance suggest management directed at 1 species should be beneficial for the other. Thus, efforts to conserve early successional communities would be appropriate (Chapter 10).

CHAPTER THREE

HISTORICAL PATTERNS IN DISTRIBUTION AND ABUNDANCE: A GEOSTATISTICAL APPROACH

Point estimates of animal abundance are typically autocorrelated in space (Legendre 1993), meaning counts conducted in close proximity likely are more similar than counts located farther apart (Robertson 1987). This relationship between point estimates, if quantified, can be useful in discerning animal abundance at unknown points between survey locations, especially across large spatial scales (McKenney et al. 1998). Geostatistics is the suite of analytic techniques suited to incorporating this autocorrelation in interpolations of species distribution and abundance (Isaaks and Srivastava 1989, Liebhold et al. 1993).

Kriging, a geostatistical technique for spatial interpolation, has been used to discern the distribution and relative abundance of numerous taxa, including various avian species (Sauer and Droege 1990; Sauer et al. 1994; Villard and Maurer 1996; Stralberg and Bao 1999; Hatfield et al., *Internet report*), moose (*Alces alces*, McKenney et al. 1999), white-tailed deer (*Odocoileus virginianus*, Nesslage and Porter 2001), marine fish (halibut *Hippoglossus stenolepis*, Pelletier and Parma 1994; herring, Maravelias and Haralabous 1995; sardine *Sardinox sagax*, Fletcher and Sumner 1999), crustaceans (Maynou et al. 1996), and sea urchin (*Tetrapygus niger*, Rodriguez and Farina 2001). Most examples of abundance kriging, however, come from the entomological field (e.g., Kemp et al. 1989; Schotzko and O'Keefe 1989; Gage et al. 1991; Liebhold et al. 1992; Hohn et al. 1993; Midgarden et al. 1993; Gribko et al. 1995; Sharov et al. 1995, 1996; Nicholson and Mather 1996; Crist 1998; Ellsbury et al. 1998; Estrada-Pena 1998, 1999).

Kriging is one of the better spatial interpolation techniques in that it is an unbiased estimator (or predictor) of grid values and it minimizes error variance (Isaaks and Srivastava 1989, Cressie 1993). Kriging provides a weighted average for a given estimated point, based on a spatial relationship and covariation between surrounding data. The form of this prediction is determined by variogram modeling (also known as semivariance analysis).

Variograms are graphic displays of the correlation (semivariance) between *z*-values of points, plotted against the distance between points. The *y*-intercept of variograms should, theoretically, equal 0. A positive *y*-intercept is described as a *nugget*. Rarely is a nugget effect absent in ecological data, principally because data are measured with error and some degree of autocorrelation occurs at scales smaller than were examined. The *sill* is where the semivariance asymptotes and indicates the distance at which point estimates are no longer autocorrelated spatially.

I developed numerous spatially-explicit models of Northern Bobwhite distribution and relative abundance with kriging techniques. These models estimate and visually present annual relative abundance between 1967 and 1998, which includes the period in which bobwhite exhibited their greatest decline. These annual maps of relative abundance allowed for an instantaneous view of population change (Villard and Maurer 1996, McKenney et al. 1998). I expected change to be most evident spatially in years in which abundance declined most.

METHODS

Historical Periods of Abundance

Bobwhite call counts were analyzed to discern historical periods in abundance. Main sources of variation between years were extracted by S-mode principal components analysis (PCA), reducing the number of variables (years in this case) into a linearized combination of orthogonal (i.e., non-correlated or independent) traits. S-mode PCA differs from the more familiar R-mode in that the variables reference years, cases reference survey locations, and the fixed entity is the number of bobwhites counted (Richman 1986). The resulting eigenvectors subsequently described independent periods of historical bobwhite abundance in Illinois.

Significance of component eigenvalues and loadings was determined with parallel analysis (Franklin et al. 1995). I modified the SAS (SAS Institute, Inc., Cary, North Carolina, USA) script provided by Franklin et al. (1995) to determine the 95th percentile eigenvalues in S-PLUS (MathSoft 1999); those eigenvalues from the test data exceeding these 95th percentile eigenvalues were considered significant.

Varimax-rotation of component loadings was applied to increase interpretability of eigenvectors. Because of the large number of missing counts and the relatively poor performance of PCA in defining periods of state-wide abundance (as opposed to the periods defined for the quail range), I used “break-points” in plots of standardized estimates of abundance to further assist in defining periods.

Geostatistical Analyses

Bobwhite call counts were transformed by application of a logarithm (with an offset of 1) or a square root to more properly conform to a normal distribution. For mapping purposes, a back transformation was applied when necessary to approximate the original counts (Robertson 1998). Semivariance analysis was conducted with the following model:

$$\gamma(h) = [1 / 2N(h)]\sum [z_i - z_{i+h}]^2; \qquad \text{(Equation 3.1)}$$

where $\gamma(h)$ is the semivariance for interval distance class h, z_i is the sample value (count) measured at point (stop) i, z_{i+h} is the sample value measure at point $i+h$, and $N(h)$ is the total number of coupled samples for the lag interval h (Robertson 1998). The semivariance, $\gamma(h)$, is essentially half of the average squared differences summed between paired stop counts.

Distances between each possible combination of paired stop-counts were accumulated into a distribution of distances that was then discretized into classes by the formula:

$$\text{class} = \text{INT}(D/DI)+1; \qquad \text{(Equation 3.2)}$$

where D is the distance between pairs, DI is the lag class distance interval, and INT is the integer of the ratio between distance and lag class. The lag class is a uniform interval of the lag distance, which is the range over which the semivariance was calculated. The lag distance was preliminarily set at 80% of the maximum distance between the farthest pair of stops. A semivariance statistic was calculated for each lag class and then visually conveyed by graphing all *h*'s versus all semivariances for each interval class (this graph is a variogram, or sometimes a semivariogram).

Five types of linear models (spherical, exponential, linear, linear to sill, and Gaussian) were fitted to the semivariance-by-lag data. The final linear model was 1 of the 5 maximizing both the proportion of explained spatial variance and coefficient of determination, while minimizing the reduced-sums-of-squares. I assessed whether azimuth direction influenced bobwhite distribution by calculating anisotropic semivariances (semivariance calculated along different axes) and compared their model fit statistics to isotropic semivariances, which ignored potential trends in direction. When anisotropic semivariances fit the data better, I modeled both iso- and aniso-tropic models. Additional detail regarding semivariance modeling is provided by Isaaks and Srivastava (1989), Cressie (1993), and Robertson (1998).

The modeled spatial autocorrelation (the variogram) was then used in a kriging procedure to interpolate counts (abundance) of bobwhite. Kriging provides an optimal interpolation estimate for any given location as well as a variance estimate for the interpolated value (Isaaks and Srivastava 1988, Robertson 1998) and thus is preferable to other interpolation methods such as inverse distance weighting. Kriging interpolated values for each 500 × 500-m pixel in a uniform grid covering Illinois, with nearest neighbor values weighted by distance and the degree of autocorrelation present for that distance (as defined by the variogram model). The neighborhood to weight interpolations was set to 16. The resultant map was subjected to a cross-validation procedure to identify poorly interpolated portions of the state.

All geostatistical analyses were conducted within GS$^+$ (Gamma Design Software, Plainwell, Michigan, USA) and the interpolations were exported to ArcView for further manipulation. Density-change surfaces (McKenney et al. 1998) were created by calculating the difference between adjoining historical periods, for both state-wide and quail range interpolations. Changes in distribution from one time period to another were quantified with Pearson's product-moment correlation.

RESULTS

Historical Periods

Three distinct periods in abundance, connected by 2 transitional phases, were suggested by the principal component analysis for the quail range (Table 3.1). The eigenvectors for the distinct periods explained 42.6% of the variation in historical abundance, whereas the transitional periods contributed an additional 10.6% of explained variance. The first principal component, PC1, explained 25.0% of the total variance and possessed strong positive loadings from 1993-1998. The second principal component, PC2, explained 10.1% of total variance and possessed strong positive contributions from 1982-1988. The third principal component, PC3, explained 7.5% of total variance and had strong loadings for 1976 and 1977. While 1975 had a substantial correlation with PC5, its relatively large loading on PC3 suggested inclusion with 1976 and 1977 for sake of simplicity. The initial year of the call count survey, 1974, was excluded from this analysis because it appeared to be poorly represented compared to subsequent years (this is supported by other data suggesting a dissimilarity to subsequent years). However, when

Table 3.1. Varimax-rotated principal components, ordered by time, describing historical periods of Northern Bobwhite abundance in the quail range of Illinois. Only loadings ≥ |0.300| are shown and only loadings ≥ |0.487| are significant at $P < 0.05$. Loadings defining periods are highlighted in bold. Percent is the percentage of total explained variation provided by the eigenvector. h^2, the communality, is the proportion of variation explained by the eigenvectors. Abundance data were derived from the Illinois Department of Natural Resources call count surveys.

Component	3	4	2	5	1	
Eigenvalues	1.81^{*}	1.33	2.43^{*}	1.20	6.00^{*}	
Percent	7.5	5.6	10.1	5.0	25.0	
Eigenvectors	1970s	→	1980s	→	1990s	h^2
1975	**0.397**			0.493		0.485
1976	**0.797**					0.666
1977	**0.744**	-0.298				0.653
1978	0.346	**-0.705**				0.672
1979		**-0.695**				0.516
1980		**-0.427**	0.367		0.316	0.436

Table 3.1. Continued.

Comp-onent	3	4	2	5	1	h^2
1981		**-0.389**	0.383		0.345	0.443
1982			**0.668**			0.512
1983			**0.618**			0.471
1984			**0.655**			0.455
1985			**0.666**			0.475
1986			**0.636**	0.311		0.527
1987			**0.502**	0.302		0.402
1988			**0.634**			0.523
1989			0.386	**0.706**		0.685
1990				**0.619**		0.493
1991				**0.687**		0.555
1992				**0.629**	0.356	0.536

Table 3.1. Continued.

Component	3	4	2	5	1	h^2
1993				0.421	**0.514**	0.540
1994					**0.621**	0.496
1995					**0.669**	0.522
1996					**0.755**	0.65
1997					**0.665**	0.508
1998			0.317		**0.647**	0.552

[*] Significant eigenvector, $P < 0.05$.

the analysis was run including data from 1974, 1974 and 1975 were included in a single component with 1976 and 1977.

The transitional phases were explained by PC4 and PC5. PC4 explained 5.6% of total variance and was the only eigenvector with strong negative loadings; it defined the transition period from 1978 to 1981 and connected PC3 (the late 1970s) to PC2 (the 1980s). PC5, the weakest eigenvector, explained 5.0% of total variance and defined the transition phase from 1989 to 1992, connecting PC2 to PC1 (the 1990s).

With PCA, state-wide abundance of bobwhite was best described by 7 periods (Table 3.2). However, low communalities (total variance described by the jth variable over the K principal components) for each year and inconsistency in the loadings, especially in later years, necessitated use of visually-assessed “break-points” to divide the state-wide count data into 6 periods. I divided bobwhite abundance into the following periods: the late 1960s (1967–1971), mid-1970s (1972–1978), early 1980s (1979–1983), mid-1980s (1984–1988), early 1990s (1989–1995), and late 1990s (1996–1998). The late 1980s and 1990s were characterized by large year-to-year variation in site-level abundance and, therefore, are probably better represented by both annual and period maps of distribution.

Geostatistical Analyses

Semivariance analysis indicated count data were autocorrelated state-wide in the late-1970s and early-1980s (Table 3.3). In general, models fit NABBS data (R^2s > 0.93) better than IDNR data (R^2s < 0.88), possibly due to a smaller sample size and greater

Table 3.2. Varimax-rotated principal components of North American Breeding Bird Survey Call Counts, ordered by time, describing historical periods of Northern Bobwhite abundance across Illinois. Only loadings ≥ |0.300| are listed and only loadings ≥ |0.325| are significant at $P < 0.05$. Loadings defining periods are highlighted in bold. Percent is the percentage of total explained variation provided by the eigenvector. h^2, the communality, is the proportion of variation explained by the eigenvectors.

Eigen-vectors	late 1960s	early-mid 1970s	late 1970s - early 1980s	early 1980s	mid-late 1980s	mid 1990s	late 1990s	h^2
Eigen-values	1.77^*	2.49^*	1.47^*	1.28	5.99^*	1.28	1.07	
Percent	5.6	7.8	4.6	4.0	18.7	4.0	3.4	
1967	**0.658**							0.587
1968	**0.625**							0.604
1969	**0.701**							0.637
1970	**0.311**							0.517
1971	**0.558**	0.336						0.499
1972		**0.551**						0.622
1973		**0.697**						0.574
1974		**0.666**						0.539
1975		**0.625**						0.583
1976		**0.589**				-0.327		0.502

Table 3.2. Continued.

Eigen-vectors	late 1960s	early-mid 1970s	late 1970s - early 1980s	early 1980s	mid-late 1980s	mid 1990s	late 1990s	h^2
1977		**0.429**						0.629
1978		**0.436**						0.530
1979			**0.703**					0.553
1980			**0.481**					0.495
1981			**0.471**					0.615
1982			**0.635**					0.606
1983				0.728				0.628
1984						-0.565		0.527
1985					**0.736**			0.594
1986						-0.355		0.613
1987					**0.613**			0.617
1988					**0.438**			0.590

Table 3.2. Continued.

Eigen-vectors	late 1960s	early-mid 1970s	late 1970s - early 1980s	early 1980s	mid-late 1980s	mid 1990s	late 1990s	h^2
1989								0.623
1990								0.583
1991					0.463			0.490
1992								0.674
1993				0.483				0.600
1994								0.586
1995						**-0.456**		0.557
1996						**-0.708**		0.684
1997					0.301		**0.339**	0.598
1998							**0.761**	0.669

[*] Significant eigenvector, $P < 0.05$.

Table 3.3. Semivariance model parameters for quail range and state-wide measures of abundance, as defined by Illinois Department of Natural Resources (quail range) and North American Breeding Bird Survey (state-wide) call count data, respectively. Nugget is the unexplained spatial variance, usually attributed to measurement error or variance at scales smaller than the smallest distance between survey sites. Sill is the total explained variance. Range is the distance over which counts are significantly correlated. R^2 is a measure of model fit, whereas reduced sums of squares is a measure of the remaining unexplained variation.

Period	Model	Nugget (C_o)	Sill (C_o+C)	Range (km; A_o)	R^2	Reduced Sums of Squares
Quail Range						
1970s	Exponential	0.254	0.995	51.6	0.456	0.058
|	Exponential	0.279	1.028	57.6	0.595	0.035
1980s	Exponential	0.625	1.993	1,385.4*	0.768	0.136
|	Exponential	0.650	2.548	2,272.2*	0.850	0.082
1990s	Exponential	0.556	1.113	208.5	0.877	0.020
State-wide						
1967-1971	Exponential	0.527	1.134	354.0	0.953	0.010
1972-1978	Exponential	0.648	1.533	1,215.9*	0.930	0.019
1979-1983	Spherical	0.399	2.304	2,892.3*	0.932	0.078
1984-1988	Spherical	0.462	1.382	475.1	0.967	0.023
1989-1995	Spherical	0.545	1.276	433.2	0.994	0.002

Table 3.3. Continued.

Period	Model	Nugget (C_o)	Sill (C_o+C)	Range (km; A_o)	R^2	Reduced Sums of Squares
1996-1998	Spherical	0.713	1.511	1,293.0*	0.994	0.001

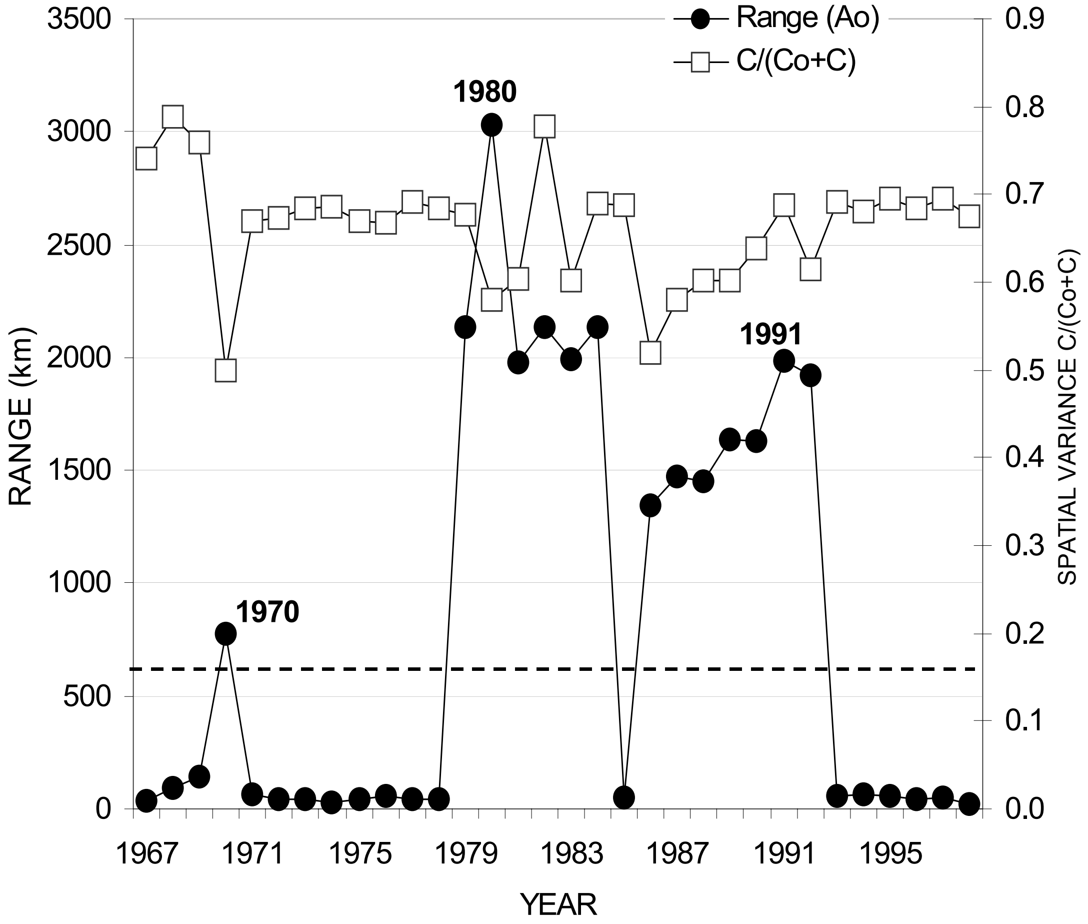
* Periods where autocorrelation existed range- or state-wide suggest an over-riding influence such as weather on bobwhite abundance.

annual variability in the IDNR data. For 3 of 33 years (1982, 1986, 1993), anisotropic models fit NABBS better than isotropic models.

Spatial models explained 65 ± 2% of the annual variance in NABBS count data. These models indicated counts were typically autocorrelated within 205.7 ± 46.8 km (range = 8.7 km in 1975 to 711 km in 1983 and 1985) (Fig. 3.1). The historical periods in abundance in the quail range (from IDNR data) were interpolated to visually express the 3 periods and 2 transitional phases (Fig. 3.2); 6 state-wide periods (from NABBS data) were mapped (Fig. 3.3). An anisotropic model was warranted when describing the autocorrelation structure in the period 1967–1971.

Change analysis, or analysis of the spatial differences between periods, indicated the greatest state-wide change occurred between the 1972–1978 and 1979–1983 periods (Table 3.4). The most obvious changes occurred along the northern portion of the historical quail range (i.e., central Illinois). Positive mean changes indicated declining abundance between subsequent periods, whereas negative means indicated increasing abundance. The IDNR call count data were somewhat contradictory to the NABBS data, exhibiting opposite patterns in change between early and late periods, but only because the periods were defined somewhat differently. The positive increase in the quail range between 1977 and 1982 reflects a much greater increase after 1980 than the decrease prior to 1980. Generally distribution of bobwhite was relatively stable from one period to the next, whereas periods separated far in time differed substantially in their areas of shared abundance (Table 3.5).

Figure 3.1. Annual extent (km) in spatial autocorrelation (Range A_o) and degree of explained spatial variance ($C/(C_o+C)$) in North American Breeding Bird Survey counts of Northern Bobwhites. Filled circles above dashed line indicate years in which bobwhite counts were autocorrelated state-wide. Dashed line is the North-South distance for Illinois.



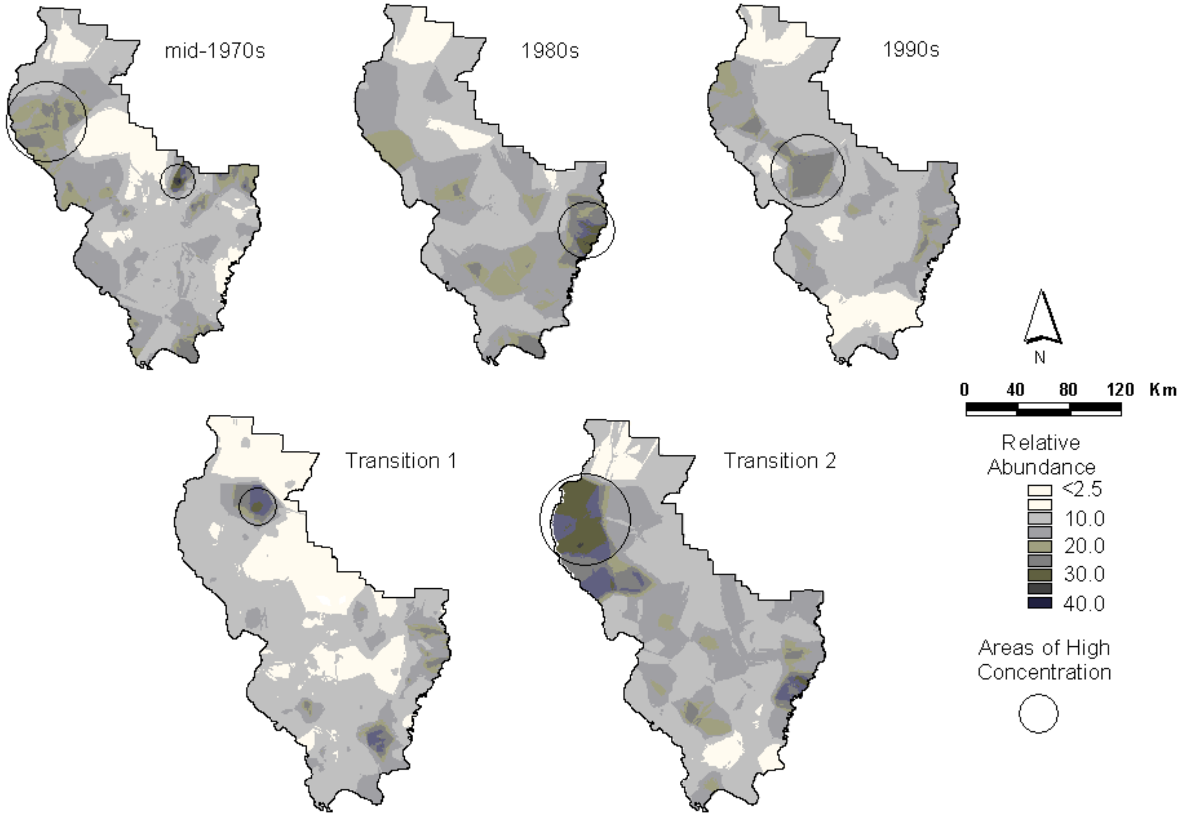


Figure 3.2. Historical distribution of Northern Bobwhite in the quail range of Illinois, as determined from Illinois Department of Natural Resources (IDNR) spring call count surveys. Relative abundance is the number predicted per site following IDNR protocol.

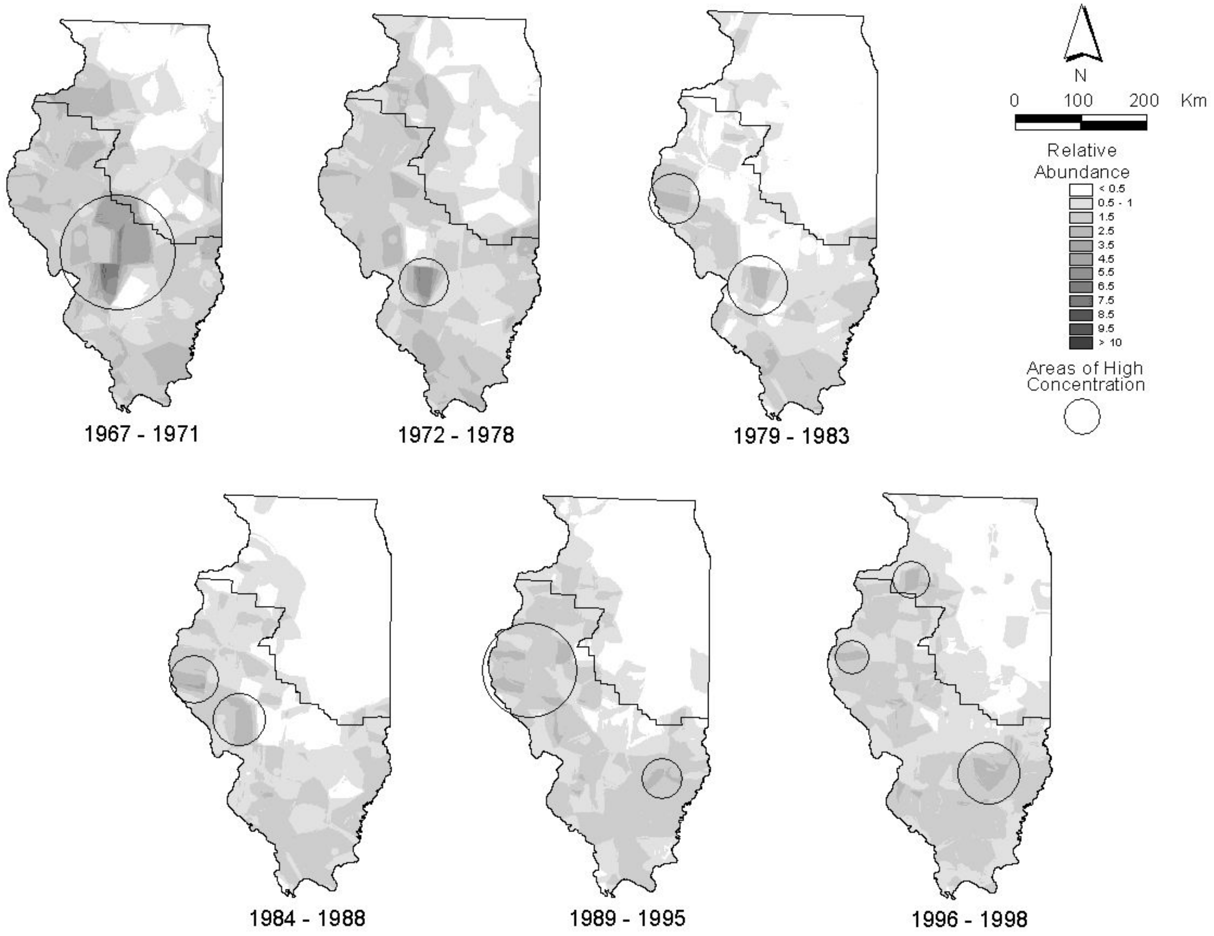


Figure 3.3. Historical distribution of Northern Bobwhite across Illinois, as determined from North American Breeding Bird Surveys. Relative abundance is the number predicted per site following NABBS call count protocol.

Table 3.4. Moments of change between periods in Northern Bobwhite abundance, as defined by state-wide North American Breeding Bird Survey and quail range Illinois Department of Natural Resources call counts, in Illinois. Change in the quail range was analyzed only between periods, and did not include the 2 transition periods. Units are in interpolated counts.

Change Period	$\bar{x}$ (SD)	Change Direction	Minimum	Maximum
Statewide				
1971–1972	0.247 (0.779)	-	-1.846	7.334
1978–1979	0.466 (0.451)	-	-1.229	3.444
1983–1984	-0.085 (0.280)	+	-1.286	1.600
1988–1989	-0.109 (0.344)	+	-2.014	1.660
1995–1996	-0.050 (0.255)	+	-1.826	1.155
Quail Range				
1977–1982	-1.252 (5.995)	0	-28.428	21.243
1988–1993	2.006 (5.304)	-	-17.893	17.109

Table 3.5. Correlation matrix between periods of spatially-explicit representations of Northern Bobwhite abundance across Illinois and within the historical quail range, as derived from North American Breeding Bird Survey and Illinois Department of Natural Resources call count data, respectively. The correlation coefficients represent the degree of similarity between spatial representations of bobwhite distribution.

State-wide	1967–1971	1972–1978	1979–1983	1984–1988	1989–1995	1996-1998
1967–1971	1.000					
1972–1978	0.636	1.000				
1979–1983	0.439	0.741	1.000			
1984–1988	0.346	0.604	0.826	1.000		
1989–1995	0.325	0.476	0.627	0.747	1.000	
1996-1998	0.285	0.440	0.572	0.627	0.857	1.000

Quail Range	1975–1977	1978–1981	1982–1988	1989–1992	1993–1998
1975–1977	1.000				
1978–1981	0.464	1.000			
1982–1988	0.346	0.528	1.000		
1989–1992	.	.	0.458	1.000	
1993–1998	0.175	.	0.448	0.628	1.000

DISCUSSION

Bobwhite abundance was autocorrelated over large areas of Illinois, and the strength of this autocorrelation varied over time. For nearly half of the years spatial autocorrelation extended state-wide. Autocorrelation over such large distances is likely due to climatic perturbations (i.e., the Moran [1953] Effect; Pollard 1991; Hanski and Woiwood 1992; Ranta et al. 1995*a*,*b*, 1997; Sutcliffe et al. 1996) rather than dispersal or predators keying on prey hotspots (Bjørnstad et al. 1999*a*). Climate, a density-independent factor, typically affects large areas simultaneously, whereas dispersal and predation are locally restricted. This is especially so for bobwhite, which are rather sedentary (Chapter 9) and are the exclusive focus of few, if any, predators.

The nugget, or the measure of unexplained spatial variance, often was large, comprising as much as half of the variance. This unexplained variance is due to 1 of 2 causes, observer sampling error or spatial autocorrelation at intervals smaller than the smallest interval in the study. Sampling error is certainly a concern with bird counts, as noted in Chapter 1. However, it is likely much of this variation can be explained by unmeasured spatial autocorrelation at distances smaller than measured for this study. In Chapter 7, I modeled abundance after accounting for spatial autocorrelation, as in this chapter. I found significant small-scale spatial autocorrelation occurred within a neighborhood size of ~44 km, a tenth of the smallest distance observed in this chapter.

Koenig (2001), in a review of spatial autocorrelation in wintering birds of North America, reported significant autocorrelation up to 250 km for bobwhite. Koenig’s test statistic for measuring correlation indicated that while significant, correlation was still low. This may be a function of his analysis methods, in that he assessed mean autocorrelation over a span of 30 winters. As my results demonstrated, the degree of autocorrelation in abundance varies over time and thus likely increases to much higher levels as environmental conditions change.

Patterns in Historical Abundance

Approximately two-thirds of the variance in annual abundance could be explained spatially. Interpolations demonstrated a severe contraction in the distribution of quail during the late-1970s, which is explained in Chapter 6 as being due to severe winter snowfall between 1977 and 1979. The most abundant populations in the late 1960s were situated in the central portion of the historical quail range. The late-1970s saw the decimation of quail from the northern and central portions of Illinois, except for the hilly Driftless Section of northwest Illinois. Large parts of the historical quail range were affected too, with areas where quail were most abundant in Illinois only 10 years earlier notably hard hit in the decline. The 1990s saw bobwhite populations increase throughout their Illinois range, re-occupying large areas of depauperate habitat.

Interestingly, bobwhite populations appeared sporadically after the late-1970s throughout the east-central portion of Illinois, resuming some of the abundance they once exhibited in the late-1960s in an area of the state dominated by corn agriculture. Whether bobwhite dispersed into these areas from the quail range or Indiana, or persisted at very low numbers through the severe winters of the late-1970s is unclear from these interpolations. Breeding bird surveys in areas of northeastern Illinois continued to report bobwhite throughout the period of severe winter weather and immediately after the resumption of normal winters, suggesting that pockets of bobwhite likely persisted, but at much lower levels of abundance.

Within the quail range, bobwhite during the 1970s were most abundant in the northeastern portion (Shelby County); in the 1980s they appeared evenly distributed, with the most abundant populations located in the east-central portion of the quail range (Edwards, Wabash, White counties). The transition phase between the 1970s and 1980s indicated most populations, except those in Fulton, McDonough, and Schuyler counties, declined substantially. The largest populations in the quail range today occur in the west-central and Wabash Border areas, whereas newly depauperate areas appear in the Shawnee Hills area of southern Illinois.

CHAPTER FOUR

COMPLEX DYNAMICS IN NORTHERN BOBWHITE TIME SERIES

Northern Bobwhite abundance is highly variable between years over much of the species range (Stoddard 1931:339-347, Rosene 1969:194-197, Schwartz 1974, Peterson and Perez 2000; Chapter 2). Bobwhite populations may fluctuate as much as 70% or more around the long-term mean (Roseberry and Klimstra 1984:122). Throughout much of the quail range these fluctuations appear primarily due to differences in overwinter mortality (Scott 1937, Mosby and Overton 1950, Kozicky and Hendrickson 1952, Kabat and Thompson 1963, Stanford 1972) and subsequent reproductive success (Lehmann 1953, Parmalee 1955, Robinson 1957*a*, Speake and Haugen 1960, Schemnitz 1964). As Edwards (1972) suggested, if wildlife managers can begin to predict the direction and strength of these fluctuations, management actions will be more effective.

Recognizing patterns in population abundance is a precondition for uncovering mechanisms responsible for producing them (Lindström et al. 1997). These patterns are appropriately revealed by analyses of abundance indexed as time series of annual call counts (Hassell et al. 1976, Turchin and Taylor 1992).

The first step in this time-series analysis is the selection of a suitable (class of) mathematical model(s) (Box and Jenkins 1970, Brockwell and Davis 1987). Analysis of time series follows 2 general approaches. One approach, the frequency domain, concerns itself with the examination of the dominant periodicities or cyclical patterns in a time series. Conversely, time-domain analysis examines the structural pattern of a time series, analyzing the values of a process directly. Combining both approaches is often useful in gleaning a better understanding of the data series. While I conducted frequency domain analyses (e.g., spectral analysis), I confined my final analyses to the time domain due to the subjective nature of period determination in spectral analysis and shortness of the time series causing poor resolution of examined spectra.

I examined temporal patterns of variability in bobwhite abundance in Illinois, discerning whether this variability was periodic. Periodicity in the bobwhite was reviewed in greater detail by Thogmartin et al. (2002); I present analyses for Illinois data sets of bobwhite here. The analyses suggested bobwhite dynamics in Illinois and other states at the periphery of their range were cyclic due to a combination of density-dependence and occasional environmental perturbations. I extend the analyses of Thogmartin et al. (2002) to include modeling dynamics of bobwhite abundance as a function of their past history. I also assessed direct- and delayed-density dependence in bobwhite populations in Illinois. Turchin (1990) suggested significant negative partial autocorrelations may indicate density-dependent mortality, which Roseberry and Klimstra (1984) suggested occurred at high densities in bobwhite. I also assessed whether temporal dynamics were synchronous over space by calculating synchrony for cycling populations of bobwhite across Illinois and for populations within regions of similar periodicity.

I assessed whether cyclic populations occupied habitat of different composition and configuration than non-cyclic populations. I hypothesized that non-cyclic populations would occur in landscapes with large contiguous tracts or in areas where row crop or wood cover was the dominant land cover. Where favorable land use practices occurred in suitable amounts (Chapter 7), cyclicity would be expected.

METHODS

I examined 4 data sets for evidence of density dependence, cyclicity, and synchrony in bobwhite population dynamics. These data sets included Roseberry and Klimstra's (1984) surveys of bobwhite in a southern Illinois study location (1954–1979), CBC counts from 1967–2000, Illinois harvest from 1975–1998, and NABBS counts from 1967–1998.

Cyclicity

Because of the sparsity of bobwhite at individual NABBS survey stops in Illinois (Chapter 2), I summarized counts for each route. Since population dynamics relate to multiplicative processes (Williamson 1971), I log-transformed (log[COUNT + 1]) total annual counts to stabilize variances (Sen and Srivastava 1990). For time series of routes with gaps in the data, I averaged the neighboring data values when the gap was only a single year. Time series with gaps ≥ 2 yrs were excluded from analyses. Routes were also excluded when the time series possessed ≥ 3 1-yr gaps or ≥ 3 yrs with zero counts. To insure a lengthy period for analysis, only routes extending ≥ 20 yrs were included.

Detection of temporal autocorrelation for each time series (i.e., correlation within a single time series) was accomplished with lagged scatter plots, autocorrelation function

(ACF) plots, and partial autocorrelation function (PACF) plots (Brockwell and Davis 1987). Cyclicity of the time series was assessed by identifying recurring peaks and valleys in the ACFs. Strong evidence for cyclicity occurred when multiple lags exceeded Bartlett's line, which is derived from convergence of sample correlation coefficients to the normal distribution (Lindström et al. 1997). Weaker evidence for cyclicity, quasi-cycles (Nisbet and Gurney 1982), was suggested when recurring patterns were observed, but the lagged autocorrelations did not reach significance. Time series with no significant lags or obvious patterns in either the ACF or PACF plots were identified as random. Pseudo-periodic cycling with phase-forgetting was verified if $\phi_1^2 + 4\phi_2 = C < 0$, where ϕ_n is the model coefficient for the first and second model parameters.

Synchronicity

I implemented a nonparametric covariance function to examine whether bobwhite populations were synchronous in their dynamics and, if present, whether these synchronous dynamics decayed with distance (Bjørnstad et al. 1999*a*,*b*). I used a nonparametric procedure (S-PLUS function Sncf; http://asi23.ent.psu.edu/) because no theory exists as to the functional form of a relationship between synchronous dynamics and distance decay. In addition to examining all time series together, I examined time series by region, looking for within-region synchronicity. I suspected, after inspection of the regional variation in period length, that bobwhite in the central and southern portions of the state may be synchronized within, but not between regions.

Time-series Models

Dynamics of each time series were modeled as a function of their own past history by fitting an AutoRegressive Integrated Moving Average (ARIMA) model. The autoregressive (AR) aspect refers to the importance or weight (ϕ) of previous values (x_{t-p}) in predicting the current value, and is usually constrained between -1 and 1. The moving average component is a weighted (θ) average of values dependent on initial random drawings and portions of previous random drawings. The ARIMA (*p*, *d*, *q*) approach assumes a probability model generating the time series data, and is of the form:

$$x_t - \phi_1 x_{t-1} - \ldots - \phi_p x_{t-p} = \varepsilon_t - \theta_q \varepsilon_{t-1} - \ldots - \theta_q \varepsilon_{t-q}$$

(The autoregressive components are typically written on the left hand side of the equation by convention).

Order of the model for the AR and MA components was identified by *p* and *q*, respectively. The integrated component (*d*) identified non-stationary aspects of the time series; because the data were detrended previous to the ARIMA modeling, $d = 0$ and thus the model devolved to an ARMA process (without prior detrending, $d \Leftrightarrow 1$).

Transformation and detrending promote *stationarity* (i.e., equal mean and variance over time) in non-stationary data sets, a requirement for time-series analysis. Only 4 of the 26 time series exhibited a relatively constant abundance prior to detrending, and only 2 possessed constant variance. To insure stationarity, several detrending techniques were employed. Residuals from first and second order polynomial regressions, as well as from local (LOESS) regression, were determined. The residual time series with positive autocorrelations at higher lags were rejected for those with positive, zero, or negative correlations at smaller lags.

There is no straightforward way to deduce the correct order for *p* and *q*. I followed the protocol for identifying proper order of the AR and MA components described by Brockwell and Davis (1987). First, preliminary inspection of ACF and PACF plots indicated initial values for *p* and *q*. Pankratz (1983) provided additional, general recommendations for deducing appropriate model parameters from these plots. The prime criterion for model selection occurred by iterating the model at each combination of *p* and *q* such that the final model possessed the lowest AICc, the small-sample Akaike's Information Criterion (McQuarrie and Tsai 1998). Model parameters were fitted with a nonlinear estimation routine (though the models themselves are usually linear) utilizing maximum likelihood procedures based on the Cholesky decomposition (MathSoft 1999). Standard errors were also computed, and parameters judged to not be significantly different from zero were dropped. The remaining parameters were then re-estimated for the final model(s).

Converged models with similar AICc (i.e., competing models with a difference ≤2 AICc; Brockwell and Davis 1987) were checked for goodness-of-fit. The most parsimonious model with the better goodness-of-fit was chosen as the final model. However, inference was aided by the competing models, in accordance with the Information-Theoretic approach to statistical model building (Burnham and Anderson 1998).

Standardized residual and ACF and PACF plots of the residuals were examined to insure that they were randomly distributed, indicating the model adequately accounted for temporal variance in the data. The Ljung-Box statistic was plotted for each lag as an additional check on goodness of model fit.

Density Dependence

Following Turchin (1990), I identified whether a population exhibited direct- or delayed-density dependence. Direct density dependence was identified by a negative partial correlation between counts in year t and year t-1, whereas delayed density dependence was a negative correlation between year t and year t-x, where $x > 1$.

Habitat Contiguity

I determined the amount of each of 8 land use classes (Illinois Department of Natural Resources 1996) in a 50-ha area around each NABBS survey location (total area sampled ≈ 2,500 ha). The land uses included row crop, small grain, grassland, woods, water, wetland, human built-up land (e.g., urban, transportation), and barrens. I excluded barrens (i.e., exposed soil, sandy beaches, quarries) as a category due to its very low frequency. Fifty hectares was chosen as this is the approximate listening area for each NABBS surveyor (Chapter 1). Amount of each land use within each 50 ha area was summed for each route.

I conducted a principal components analysis of the 7 land use classes. This analysis accounted for the high multicollinearity between row crop, small grain, and woods land use classes. Due to small sample size, I assessed with Wilcoxon rank-sum tests whether landscapes occupied by cyclic populations differed from landscapes occupied by non-cyclic populations. As in the previous chapter, Parallel Analysis determined significance of principal components.

RESULTS

Lagged scatter plots (Appendices 4.A, 4.B) and plots of the autocorrelation and partial autocorrelation functions (Fig. 4.1) suggested most counts were autocorrelated with abundance from the previous year. Only occasionally did this correlation extend to lags >2 (for NABBS data, for instance, twice for lag 2, 3 times for lag 3, and 4 for all other lags). Mean autocorrelation of NABBS counts was 0.336 ± 0.027 for lag 1 and 0.172 ± 0.027 for lag 2. Much of the correlation for lag 2 was due to some bleed-over from lag 1 since the mean partial autocorrelation for lag 2 was -0.01, whereas the mean partial autocorrelation for lag 1 was 0.336.

Density Dependence

Nineteen of 26 populations indexed by NABBS routes exhibited direct-density dependence (PACFs ≥ 0.392, $\bar{x} = 0.570 \pm 0.021$); another 4 possessed 1st lag PACFs equal to 0.26 or greater. Only 2 of 26 time series exhibited delayed-density dependence, but at lag 3 rather than lag 2 (PACFs at lag 3 = -0.402 and -0.443). Six time series exhibited weak delayed-density dependence, possessing lag 2 PACFs between -0.114 and -0.304.

Direct-density dependence was evident in each of the other 4 data sets. Partial

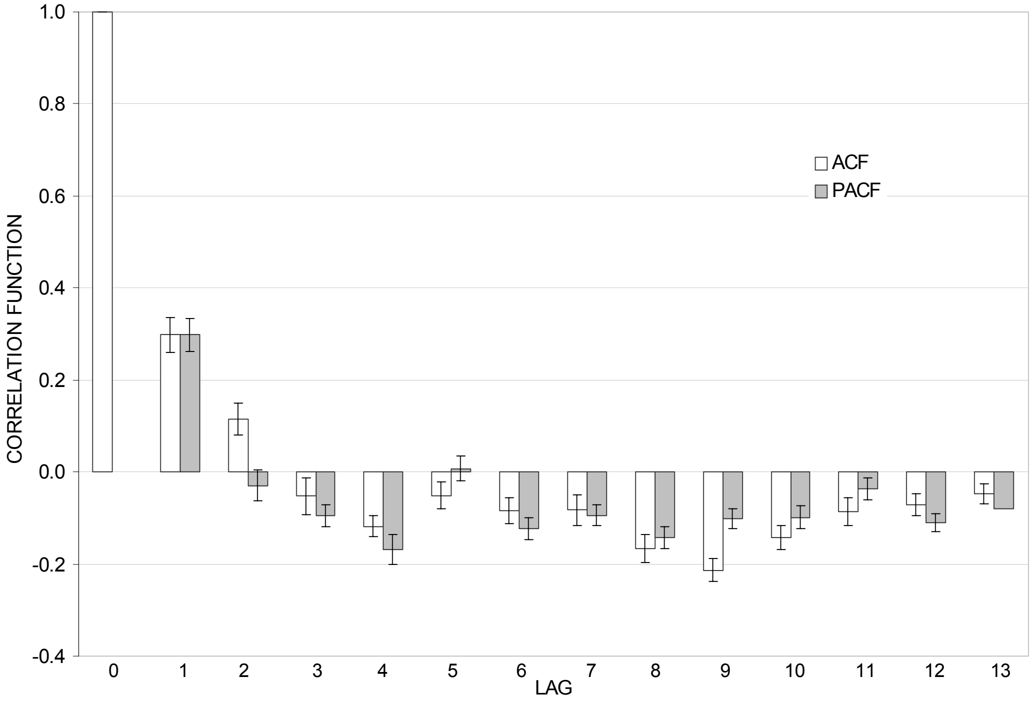


Figure 4.1. Mean autocorrelation (ACF) and partial autocorrelation (PACF) function for time-series of Northern Bobwhite abundance as determined by North American Breeding Bird Surveys. According to Nisbet and Gurney (1984), due to the short extent of the time series, correlations ≥6 are tentative. Significant correlations $\geq |0.392|$.

correlations for indices reported by Roseberry and Klimstra (1984) were 0.488 and 0.439 for March and November, respectively. Both harvest (IDNR) and winter counts (CBC) exhibited higher first lag partial correlations (ρ's = 0.531 and 0.602, respectively).

Delays in density dependence were also evident in these data sets. The November index of Roseberry and Klimstra (1984), which exhibited true cyclicity, exhibited delayed-density dependence at lags 2 and 4 (ρ's = -0.543 and -0.429). The quasi-cyclic March index did not exhibit delays in density dependence. Christmas Bird Counts exhibited a significant delay at lag 6 ($\rho = -0.319$) whereas harvest indicated delays at lag 2 ($\rho = -0.513$).

Cyclicity

Periodic Behavior.—At the time-scale I investigated (n = 21–25 years), examination of ACFs indicated periodicity in 18 of the NABBS time series. However, none of the autocorrelations exceeded Bartlett's band and thus none were definitively periodic. The NABBS time series were grouped in 2 levels of quasi-periodicity (Fig. 4.2), 1 centered around a period of 7 years ($\bar{x}_T = 6.7 \pm 0.2$, $n = 6$), the other around a period of 17 years ($\bar{x}_T = 16.6 \pm 0.4$, $n = 10$). One other time series appeared to possess a period $T = 11$, whereas another time series was suggestive of periodicity $T > 20$. Due to shortness of the time series, however, caution must be extended in interpreting these results as lags greater than lag 6 are tentative. The general form of cyclicity was quasi-periodicity with phase-forgetting (C = -0.521 for the mean route condition).

Quasi-periodicity (with phaseforgetting) was evident in the March indexed

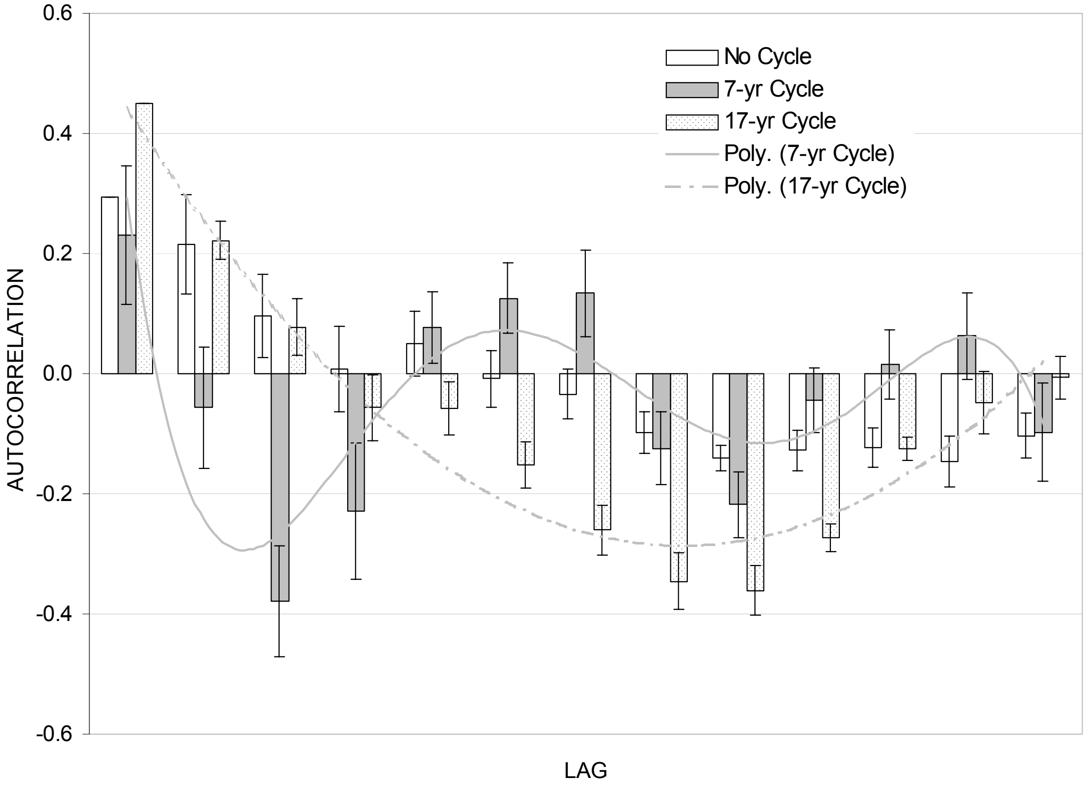


Figure 4.2. Autocorrelation function for NABBS of Northern Bobwhite in Illinois, grouped by period. Polynomials were fitted to the different classes to assist in visualizing patterns in the ACFs. Significant correlations were those ≥ │0.392│.

gathered by Roseberry and Klimstra (1984), whereas true periodicity occurred in the November population. The bobwhite populations studied by Roseberry and Klimstra cycled with a period of 8 yrs. None of the indices summed over the entire state (NABBS counts summed for the state, CBC winter counts, or IDNR harvest) exhibited evidence of cyclic dynamics.

Influence of Habitat Fragmentation.—Parallel analysis identified 3 significant principal components describing Illinois land use. At the scale and precision of analyses I conducted, I found no differences in the landscapes of cycling and non-cycling bobwhite populations (W range = 210–229, P's > 0.44). Biplots of the first 3 components indicated no discernible separation between cycling and non-cycling populations in the landscapes they occupied (Fig. 4.3).

Synchronicity

North American Breeding Bird Survey stops summarized by 10-stop increments did not exhibit substantial synchronous dynamics for the period 1967–1998; mean regional synchrony was low ($r = 0.09$; 95% CI = 0.05–0.14) and extended 174.9 km. When NABBS routes were considered, similarly low synchrony was observed ($r = 0.076$; extent = 55.6 km) (Fig. 4.4). However, once regions of similar levels of cyclicity were examined, stronger patterns in spatial synchrony became evident. Dynamics in the region of central Illinois where bobwhite cycled on approximately a 17-yr period were synchronous ($n = 9$, $\bar{x}_r = 0.36$, 95% CI = 0.21–0.52). Synchronicity increased more than 2-fold in southern Illinois, where bobwhite cycled on a 7-yr period ($n = 6$, $\bar{x}_r = 0.19$), but this increase was

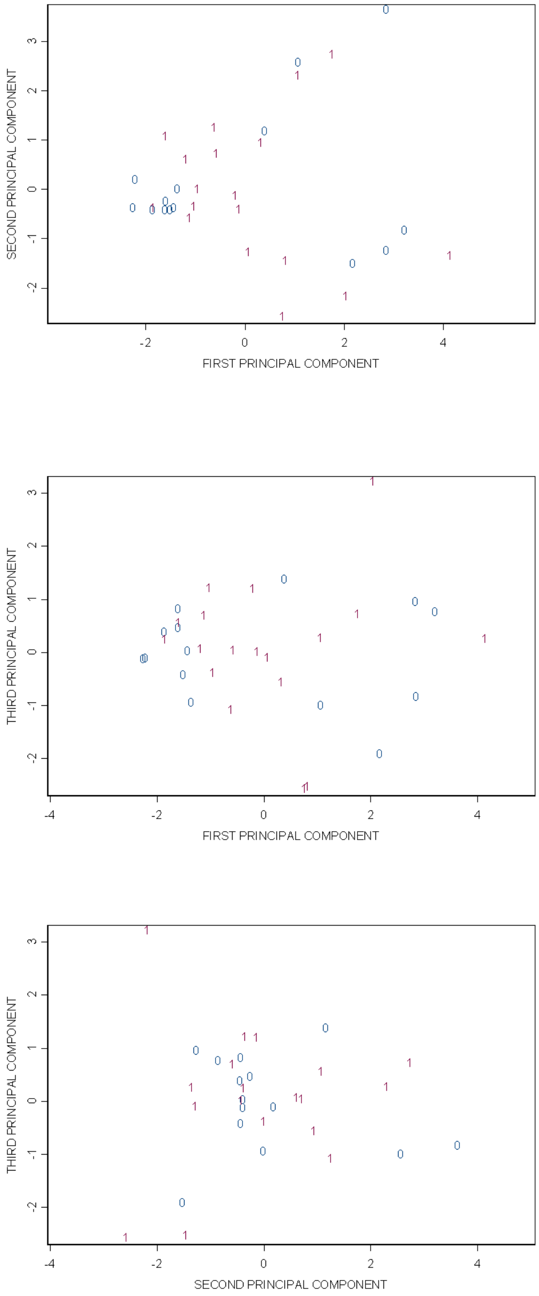


Figure 4.3. Biplots of first, second, and third principal components of land use classes in Illinois landscapes occupied by cycling (1) and non-cycling (0) Northern Bobwhite populations.

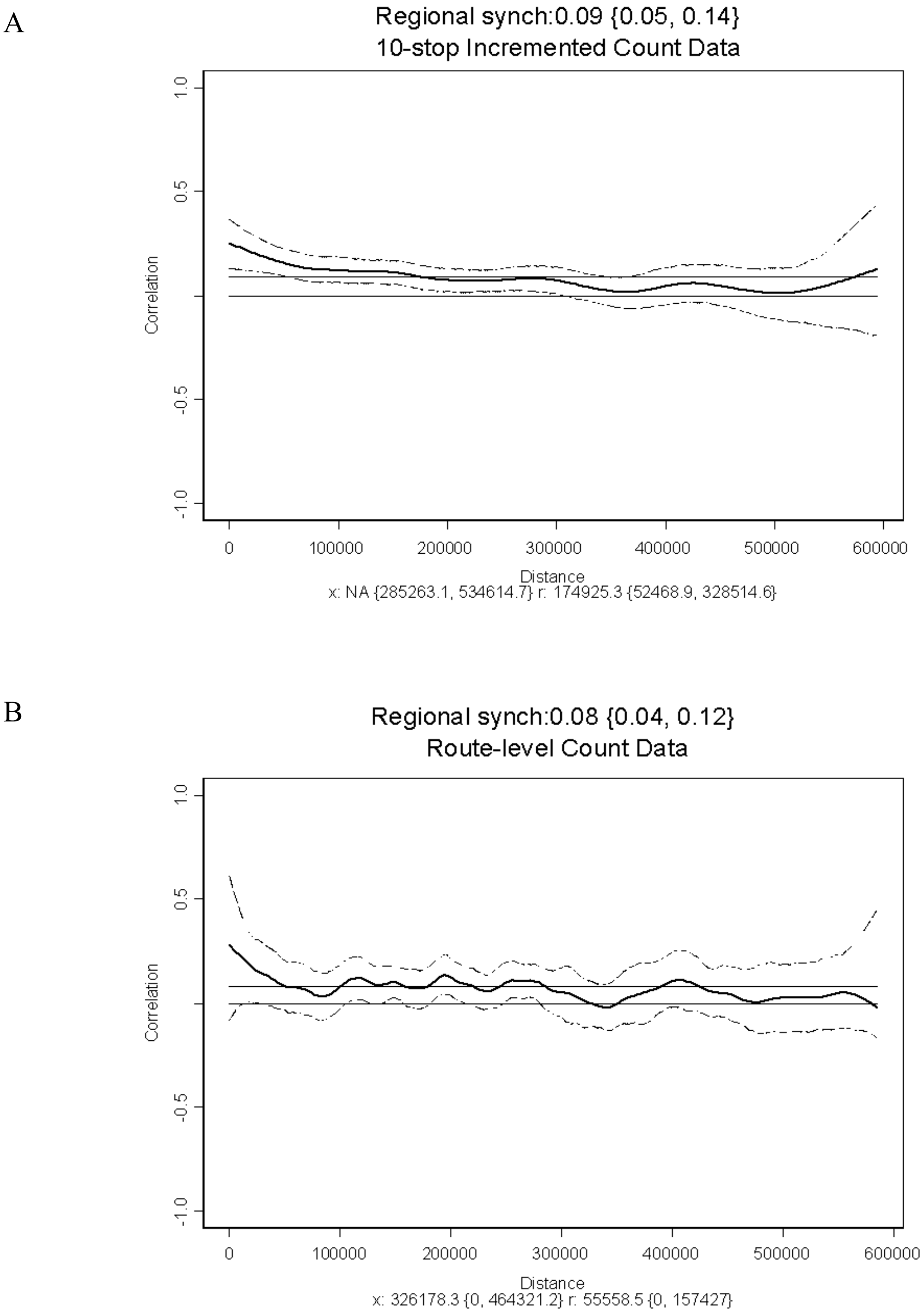


Figure 4.4. Plot of synchrony by distance for Northern Bobwhite population dynamics in Illinois. A, based on 10-stop increments of North American Breeding Bird Survey (NABBS) data. B, based on route-level NABBS data.

Table 4.1. Competing autoregression models of NABBS time series (1973–1997). Total is the time series of annual counts for the entire state, whereas Mean is the average model of the 26 time series and range is the range of observed model coefficients. AICc is the Aikike's Information Criterion corrected for small samples.

DATA	AR(1)	AR(2)	AR(3)	AR(4)	AICc
TOTAL (SE)	-0.179 (0.041)	-0.034 (0.040)	-0.274 (0.040)	-0.507 (0.041)	77.43
MEAN (RANGE)	0.153 (-0.422-0.802)	-0.136 (-0.737-0.352)	-0.127 (-0.580-0.328)	-0.174 (-0.540-0.260)	NA

not significant (-0.08–0.42).

Autoregressive Integrated Moving Average Models

Sixteen of 26 NABBS time series exhibited a significant trend (1 of which was positive) from 1973 to 1998. These trends were removed before calculation of the ARIMAs. Two time series did not possess a discernible trend; 9 were detrended by simple linear (first order polynomial) regression, indicating a temporally invariant trend; 8 were detrended by second order polynomial regression, and 7 were detrended by LOESS, both of which indicated a time-varying trend.

The typical model involved >4 parameters (4.5 ± 0.7). Only 1 model employed a moving average component, and even then the coefficient was not significant. This indicated the detrended time series were not over-differenced (i.e., the time series were adequately detrended) and the model structure devolved to an autoregression. Confidence limits on the autoregression coefficients on the ARIMA model of total transformed NABBS counts indicated only AR(1), AR(3), and AR(4) were significant (Table 4.1); the final model was: $X_t = -0.179X_{t-1} - 0.274X_{t-3} - 0.570X_{t-4}$.

Model averaging developed for the routes defined an autoregression with 4 equally weighted coefficients (Table 4.1). The first coefficient (0.153), being positive, acted to push subsequent annual abundance away from the long-term mean, whereas the negative coefficients for AR(2–4) acted to pull abundance back to the long-term mean. This to-and-fro motion of the model parameters modeled average dynamics for bobwhite in Illinois from 1973–1997.

DISCUSSION

Local bobwhite populations exhibit considerable fluctuation in size because recruitment and non-breeding season mortality is highly variable. Autoregressions of bobwhite dynamics in Illinois reflected this considerable variability. The mean autoregression for the routes was similar to the model developed by Roseberry and Klimstra (1984:159). They found AR(1) = 0.731 (compared to 0.153 for the mean AR) and AR(2) = -0.335 (versus -0.136). Their model coefficients occur within the observed range of variation in coefficients for the NABBS models. This is encouraging in that their estimates were based on annual censuses of bobwhite at a single location in southern Illinois whereas my estimates were for bobwhite throughout Illinois. C for Roseberry and Klimstra's autoregression was -0.806, indicating the potential for phase-forgetting in cycles they studied.

Direct-density dependence was common in the time series I examined whereas delays in density dependence were less common. Roseberry and Klimstra (1984) provided a thorough review of direct-density dependence in quail, which I will not reiterate here except to note that the effects of density dependence are visible in non-breeding season mortality, recruitment, and overall population rates of change. A consequence of strong direct density-dependence is stable populations, whereas delayed density effects are predicted to cause fluctuations in abundance (May 1976). For those populations exhibiting considerable cyclic variation, delayed effects on population growth occur through modifications of reproduction and/or survival (Errington 1945, Stenseth 1985, Hanski et al. 1993, Agrell et al. 1995). For bobwhite, field data demonstrating these delayed effects are lacking, but are necessary to establish the role, if any, of delayed density dependence on population cycling in this species.

Cyclicity

Thogmartin et al. (2002) reviewed evidence for the general phenomena of cyclicity in bobwhite population dynamics across the species' range. Bobwhite in Illinois are part of a band of states running from the north-central to the southwestern portion of the range wherein bobwhite generally exhibit quasi-cyclic periodicity. These quasi-cycles, which are not mathematically true cycles, but are instead cycle-like in their recurring behavior, are generally phase-forgetting (PFQC; Nisbet and Gurney 1982, Turchin and Taylor 1992). The cycles are phase-forgetting because the cycle diminishes as lag increases. Thogmartin et al. (2002) suggested environmental forcers such as aperiodic climate perturbations coupled with density dependence acted to cause periodic behavior in bobwhite abundance.

As mentioned in Thogmartin et al. (2002), lack of cyclicity in CBC winter counts, IDNR harvest, and NABBS counts summarized for the state is likely due to the averaging of populations cycling at different periods. Location-specific censuses conducted by NABBS and Roseberry and Klimstra (1984) indicated cyclic behavior in population dynamics was a common, though not universal, phenomenon for bobwhite.

Why some Illinois populations of bobwhite, as indexed at the route-level, did not cycle is still unknown; at the scale that I analyzed the effect of habitat fragmentation on propensity to cycle (Moss and Watson, *In press*), I found no evidence bobwhite populations in more contiguous landscapes differed in their likelihood to cycle. Thus, I suggest Moss and Watson's (*In press*) hypothesis may not be a universal phenomenon for all galliforms, that landscape fragmentation may not necessarily alter a species population dynamics to the extent that cyclical behavior in abundance is disrupted.

Synchronicity

The degree and extent of regional synchrony may provide insight into processes determining population dynamics across a range of spatial scales (Sokal 1979, Thomas 1991, Hanski and Woiwood 1992). Typically, synchronized dynamics are attributed to ≥1 of 3 processes. Synchrony may be due to, first, dispersal between spatially-structured populations (Maynard Smith 1974), second, the correlated effect of density-independent factors synchronizing populations with the same density-dependent structure (i.e., the Moran [1953] Effect; Hanski 1991, Royama 1992, Ranta et al. 1997, Cattadori et al. 1999, Hudson and Cattadori 1999, Koenig 1999), and third, predator-prey interactions whereby nomadic predators cause synchrony in prey fluctuations or specialist predators switch to alternative prey when their main prey declines (Korpimaki and Norrdahl 1989, Ims and Steen 1990, Small et al. 1993). Generally, dispersal acts to cause synchrony over short distances whereas density-independent and predator effects cause synchrony over much larger domains.

Kabat and Thompson (1963) believed there was no evidence supporting synchronous fluctuations in Wisconsin populations of bobwhite. However, similar to the lack of cyclicity in state-wide dynamics, failure to find synchronicity in dynamics is likely due to examination of the data at an inappropriate scale. Furthermore, the strength of synchrony may be influenced by the phase of the population cycle, being stronger when the population is in decline and weaker during population growth (Sinclair and Gosline 1997).

In this study, I demonstrated synchronous dynamics did occur within, but not between regions in Illinois and that synchrony was generally low. Paradis et al. (2000) reported weak synchrony in non-cyclic bird populations, whereas Ranta et al. (1995*a*) provided several examples of non-cyclic species in Finland exhibiting strong population synchrony. Lande et al. (1999) indicated that if there were errors in the indices of population size, the effect would be to bias observed synchrony toward lower values. Lande et al. (1999:271) wrote: “Random errors are expected to augment the variances in estimated population sizes (which appear in the denominator of a correlation coefficient), but are not expected to alter the covariance between two independently estimated populations (which appear in the denominator of a correlation coefficient).”

Ranta et al. (1995*a*) and Lindström et al. (1996) reported similar large-scale synchrony in dynamics of the galliforms Capercaillie (*Tetrao urogallus*), Black Grouse (*Tetrao tetrix*), and Hazel Grouse (*Bonasa bonasia*) in Finland. In their situation, they attributed synchrony to the combined effect of climate and dispersal. They stressed that the actual climatic factor causing synchronicity need not be the same in every year, making it difficult if not impossible to attribute synchrony to any 1 climatological process.

Either the Moran effect or predator-prey dynamics are the most parsimonious choice to explain synchronous dynamics in Illinois quail populations given that the domain of influence was >100 km and bobwhite are relatively sedentary in their annual movements. Of the 2 choices, the Moran effect probably has more weight given that the proposed causes of cyclicity in quail is climate-related perturbations (Thogmartin et al. 2002).

CHAPTER FIVE

PERSISTENCE OF POPULATIONS: EMPIRICAL EVIDENCE AND PREDICTIONS OF A STOCHASTIC DIFFUSION MODEL

To admit that species generally become rare before they become extinct,
to feel no surprise at the rarity of the species, and yet to marvel greatly when
the species ceases to exist, is much the same as to admit that sickness
in the individual is the forerunner of death -
to feel no surprise at sickness, but, when the sick man dies,
to wonder and to suspect that he died of some deed of violence.
Charles Darwin (in *The Origin of Species*)

Those who have knowledge, do not predict,
Those who predict, do not have knowledge.
Lao Tzu, Chinese philospher 604-531 B.C

Extinction is the irrevocable loss of the last local population of a species (Andrewartha and Birch 1954). Inevitably, all populations will be extirpated, and thus, all species will become extinct. However, it is the human-induced rapidity of current extinctions that is a cause for great concern.

The proximate causes of population extirpation in Northern Bobwhite are poorly understood, but likely include environmental and demographic stochasticity (Goodman 1987, Lande 1993, Sæther et al. 1998, Legendre et al. 1999), genetic deterioration or increased homozygosity (Allendorf and Leary 1986, Vucetich and Waite 1999), or social dysfunction (Vucetich et al. 1997, Legendre et al. 1999). Proximate predictors of extirpation in general include small habitat size, small population size, vulnerability to predation, guild association, diet association, large body size, and extremes in environmental variability (Lande 1993, Bibby 1995, Lawton 1995).

Carrying capacity, *k*, which is related to the area available to a population, influences population persistence (Shaffer 1981, Soulé 1987); larger populations are at less risk to catastrophic events than smaller populations. However, given unpredictable environmental fluctuations and rare catastrophic events, persistence for any population of any size can only be known in a probabilistic sense (Wissel et al. 1994).

Thus, in this probabilistic sense, predictions of the probability of and time to extinction for wildlife populations may prove useful to wildlife managers and conservation biologists. A simple extrapolation of trends in abundance will typically suffice for populations clearly in decline (Foley 1994). However, when environmental stochasticity is firmly linked to population performance, trends are less obvious and the threat of extinction is less clear. Managers of Northern Bobwhite populations in the central and southeastern U.S. are particularly concerned about local population persistence given recent declines in regional abundance (see Problem Statement, Chapter 1). Brennan (1991), for instance, predicted the extinction, or at the very least their decimation to unharvestable levels, of bobwhite within 20–40 years.

Models of population extirpation usually take 1 of 2 forms, a diffusion approximation or direct computer simulation (Halley and Iwasa 1998). Guthery et al. (2000*a*) recently simulated viability of Northern Bobwhite populations. While their predictions were not as dire as Brennan’s (1991), their results did provide additional insight into the probability of extirpation for bobwhite populations. The model by Guthery et al. (2000*a*), hereafter the Guthery model, subjected simulated bobwhite populations to seasonal weather catastrophes and harvest. These weather catastophes were modeled as random, discrete steps rather than continuous phenomena drawn from a probabilistic distribution. The Guthery model predicted a 95% persistence probability (persistence ≥100 years) for southern populations ≥100 individuals when facing summer weather catastrophes; when abundance was ≥500 individuals, populations were able to sustain winter weather catastrophes. When summer and winter weather catastrophes were combined, populations required ≥800 individuals for a 95% probability of persistence. The Guthery model indicated harvest increased the population size necessary to avert extirpation from 100 to 700 individuals in the face of summer weather catastrophes. However, harvested populations facing a winter catastrophe required fewer individuals than a similar, unharvested population, ostensibly due to compensatory mortality.

The Guthery model was a mechanistic simulation model (McCullough 1979, Xie et al. 1999) parameterized by empirically-derived values for survival rates; however, while the mean parameters may adequately represent typical bobwhite populations, the model did not incorporate realistic empirical variability. For instance, the Guthery model did not incorporate "extremely good" years in the simulations, and thus did not explicitly account for the sometimes explosive growth exhibited by bobwhite. Roseberry and Klimstra (1984:72-73), for instance, found bobwhite in southern Illinois (a mid-latitude population similar to the one modeled by Guthery and his colleagues) exhibited >300% increases in spring-fall abundance 5 times in a 26-yr period; based on the time series cited by Guthery et al. (2000*a*) for parameterizing their model, this effect would likely have been seen equally as often. While rare, these optimal years of high population growth are extremely important in saturating suitable habitat and rescuing depauperate areas through dispersal.

Guthery et al.'s (2000*a*) results from simulations suggested bobwhite exhibit regular extirpations at typical population sizes. I tested this hypothesis with an empirically-based, stochastic Markov chain model. My objectives were to estimate persistence probabilities of Northern Bobwhite populations in Illinois, incorporating stochastic uncertainty in their calculation. With this information, I estimated time to quasiextirpation (T_{qe}) for individual populations. The modeling approach I describe is empirical rather than mechanistic in nature (McCullough 1979, Xie et al. 1999) and the approach I followed offered the advantage of integrating population variables more readily than is generally possible in a mechanistic approach. As McCullough (1979:215) suggested, "a few high-order variables [e.g., abundance or an index to abundance] are all that need to be measured, since they represent the population's integration of the total complex of low-order variables [e.g., rates of reproduction and survival]."

I contrast this modeling exercise with an empirical assessment of observed extinction events. This assessment is based on counts of calling bobwhite, which are simply an index to population abundance. As such, when a population is predicted to be extirpated, this extirpation may either be real ($N = 0$) or perceived. When perceived, the population goes below a threshold below which it is no longer observed ($N \approx 0$, small). This perceived extinction is described as quasiextinction (Ginzburg et al. 1982).

METHODS

Empirical Approach

Variability.— To examine historical patterns in population variability, which have a disproportionate effect on extirpation risk, I calculated a 3-yr moving average of the coefficient of variation (CV) in bobwhite counts at each stop (Gibbs 2000) after correcting for small sample size (Sokal and Rohlf 1995). Differences in mean CV between early (pre-1980) and late (post-1980) years were tested with a 2-sample *t*-test assuming equal variances.

Local Colonization and Extirpation.— I estimated local-area colonization and extirpation probabilities from records of presence and absence in stop (IDNR) and route (IDNR and NABBS) counts. I did not assess colonization and extinction for NABBS stops given the relatively low count number and high margin for error.

Wilson and Guthery (1999) suggested temporal gaps in daily male bobwhite calling may bias estimates of abundance determined by traditional 3-min point counts. Their worst-case estimates suggested call counts immediately after sunrise may miss bobwhite 50% of the time when in fact they are present in the area around the point count. I used this information to differentiate local extirpations of bobwhite from the possibility of observers simply missing bobwhite in areas where they were present. Whereas there is a probability of 0.50 of missing bobwhite in any 1 yr, there is only a 0.25 probability (0.5^2) of missing bobwhite in 2 consecutive years at any single stop when they are present in the local area. This probability declines to 0.125 (0.5^3) for 3 consecutive years and 0.0625 (0.5^4) for 4 consecutive years. Those are based on worst-case probabilities; typically the probability of missing bobwhite when they are present is probably much smaller (Wilson and Guthery 1999).

Using this information, I defined as a local extirpation event those stops with ≥4 consecutive years of 0 counts (again, with a Type I error of, at worst, 0.0625). I assumed stops provided an independent index to local population abundance; in reality, stops do not explicitly nor independently index populations as much as they index local variability in population abundance. I limited the analysis to those stops which historically possessed ≥5 bobwhite, and in doing so eliminated transitory situations. This undoubtedly resulted in some obfuscation of the true picture of local-area extirpation; however, it also eliminated the possibility of over-estimating local probability of extirpation, and thus is a conservative estimate of extinction risk.

I constructed an empty 2-dimensional array by using possible annual colonization and extirpation probabilities as row and column headings. For each cell, I used methods of Clark and Rosenzweig (1994) to determine whether the likelihood of a corresponding pair of probabilities may explain the observed data. The value of each cell was divided by the sum of the likelihoods so that the sum of all cells equaled 1.

I also examined route-level extirpations, but for routes I defined an extirpation as any route where counts of bobwhite were 0 for ≥2 consecutive years. It is unlikely observers missed bobwhite on an entire route (n = 20 stops for IDNR call counts and n = 50 for BBS) when they were present at multiple stops. All stops and routes indicating an extirpation or colonization event were tallied and then divided by the sample size to estimate historical extirpation and colonization frequency.

Modeling Approach

Rates of Change.— Foley (1994, 1997; personal communication) provided a series of calculations for determining probability of persistence for a local population over a given time interval. Foley's approach implemented a special case of the stochastic process for long-term census data. Stochastic processes, governed by probabilistic laws (Karlin and Taylor 1981), are defined as diffusion processes (Cox and Miller 1970, Karlin and Taylor 1981, Engen and Sæther 1998) when continuous both in state (i.e., number of individuals) and time (i.e., number of seasons, generations, or years). When this random process possesses a discrete parameter and state space (i.e., extinction/persistence), the process is called a Markov Chain. Foley's diffusion process is a Markov process, meaning that the probability density function (pdf) of count n_{i+1} gven n_i does not depend on observation n_{i-1} (i.e., future counts depend only on the present count and not past counts). An additional assumption of Markov Chains is that transition from state to state is instantaneous.

The Markov chain basically satisfies the following transition matrix:

$$\begin{array}{cccc} & \text{Occupied} & \text{Unoccupied} & \\ \Pr = & \left(\begin{array}{c} \Pr[\mathit{Persistence}] \\ \Pr[\mathit{Extinction}] \end{array}\right. & \left.\begin{array}{c} \Pr[\mathit{Colonization}] \\ \Pr[\mathit{Unoccupied}] \end{array}\right) & \begin{array}{l} \text{Occupied} \\ \text{Unoccupied} \end{array} \end{array}$$

When population growth is approximately stationary (i.e., $r = 0$), Foley calculated *Time to Quasiextirpation* as:

$$T_{qe}(n_0) = \frac{2n_0}{V_r}(k - n_0 / 2) \ , \qquad \text{(Equation 5.1)}$$

whereas when r ≠ 0:

$$T_{qe}(n_0) = \frac{1}{2sr_d}[e^{2sk}(1 - e^{-2sn_0}) - 2sn_0] \ , \qquad \text{(Equation 5.2)}$$

where n_0 is the index of population abundance at the beginning of the survey, k is measured as either the mean of the upper-quartile in the range of observed n or as the maximum observed n, V_r is the variance in the random effect for r, and s is the ratio of the population growth rate to the variance in the growth rate ($s = r_d/V_r$). The parameter r_d is the expected change in n as it approaches the demographic lower and upper boundaries in abundance (i.e., local extirpation, $n = 0$, and carrying capacity, k). Variance when $r \neq 0$ was calculated as:

$$V_{re} \approx \frac{1 + r}{1 - r} V_r \qquad \text{(Equation 5.3)}$$

where ρ is the Pearson product-moment correlation coefficient of r_t and r_{t+1}.

Population abundance is often serially correlated over time, usually due to serially correlated environmental effects (Pimm and Redfearn 1988, Ariño and Pimm 1995, Halley 1996, Chapter 6). In the Foley equations, ρ represents the serial autocorrelation of environmental effects (Foley 1997). Thus, when ρ > 0, effects of the environment on bobwhite abundance carry over from 1 yr to the next. When ρ < 0, bobwhite abundance is solely influenced by current environmental effects, which may include various density-dependent or -independent factors.

Probability of Persistence.—Probability of population persistence (from the start of the census) for 100 yrs was estimated by:

$$P(t) = e^{-100/Te}. \qquad \text{(Equation 5.4)}$$

Persistence probability over the next 100 yrs, time to extinction, population rate of change, and variation in the rate of change were calculated with Foley's formulae for each NABBS and IDNR call count route in Illinois possessing sufficient data for analysis.

May (1974) suggested extinction from environmental stochasticity was likely in areas where the variance in growth rate (V_r) was greater than twice the average of r. Sites with $V_r > 2r$ were identified and mapped to determine local populations at risk. I also assessed variation in abundance in relation to abundance through simple linear regression. The standard deviation in abundance (simply the square root of V_r) was related to abundance after transformation by:

$$\log(\sqrt{V_r}) = \log(a) + b \cdot \log(x), \qquad \text{(Equation 5.5)}$$

where x is route abundance, and a (y-intercept) and b (slope) are constants. If relative variability is constant across all routes, then slope is predicted to equal 1 ($b = 1$). Deviations from unity indicate greater relative variation in abundance. Slopes <1, for instance, indicate the areas with the greatest abundance of bobwhite are relatively stable. Slope >1 suggest variability in abundance increases with abundance.

RESULTS

Empirical Approach

Variability.—Time series of bobwhite abundance exhibited tremendous annual variability (Fig. 5.1). Mean annual CV was 1.40 ± 0.66, ranging from a low of 1.23 in 1972 and a high of 1.59 in 1982. Coefficient of variation increased considerably between 1978 and 1984. Prior to 1985, mean CV was 1.27 ± 0.01; after a spike in CV in 1982, mean CV was 1.43 ± 0.01. The difference in CV for the 2 periods was significant ($t_{22} = -16.06$, $P < 0.001$).

Local Colonization and Extirpation.—Presence of quail populations has declined in Illinois since the late 1960s (Fig. 5.2). One-hundred-thirty-one extinctions occurred during the period covered by the IDNR Bobwhite Call Count survey, yielding a 0.1296 annual probability of extinction. Eighty-eight colonization events were observed (0.0870 probability). Where recolonization occurred, stops were colonized 5.4 (SE = 0.2, n = 74) yrs after initial extirpation. No bobwhite counts proceeded to extinction for any routes, however, counts for the St. Clair County route were 0 in 1986 and in Henderson County in 1985 only 12 bobwhite from 2 stops were recorded.

$$\Pr = \begin{pmatrix} \Pr[\mathit{Persistence}] & 0.0870 \\ 0.1296 & \Pr[\mathit{Unoccupied}] \end{pmatrix}$$

Extinction events were more common in the NABBS data set, ostensibly due to its inclusion of routes outside of the historical quail range. Bobwhite counts for 12 routes proceeded to extinction (Fig. 5.3). Recolonization for 5 of the routes occurred within 6.7 ± 1.9 yrs, but only 1 was maintained. The other populations proceeded quickly back to

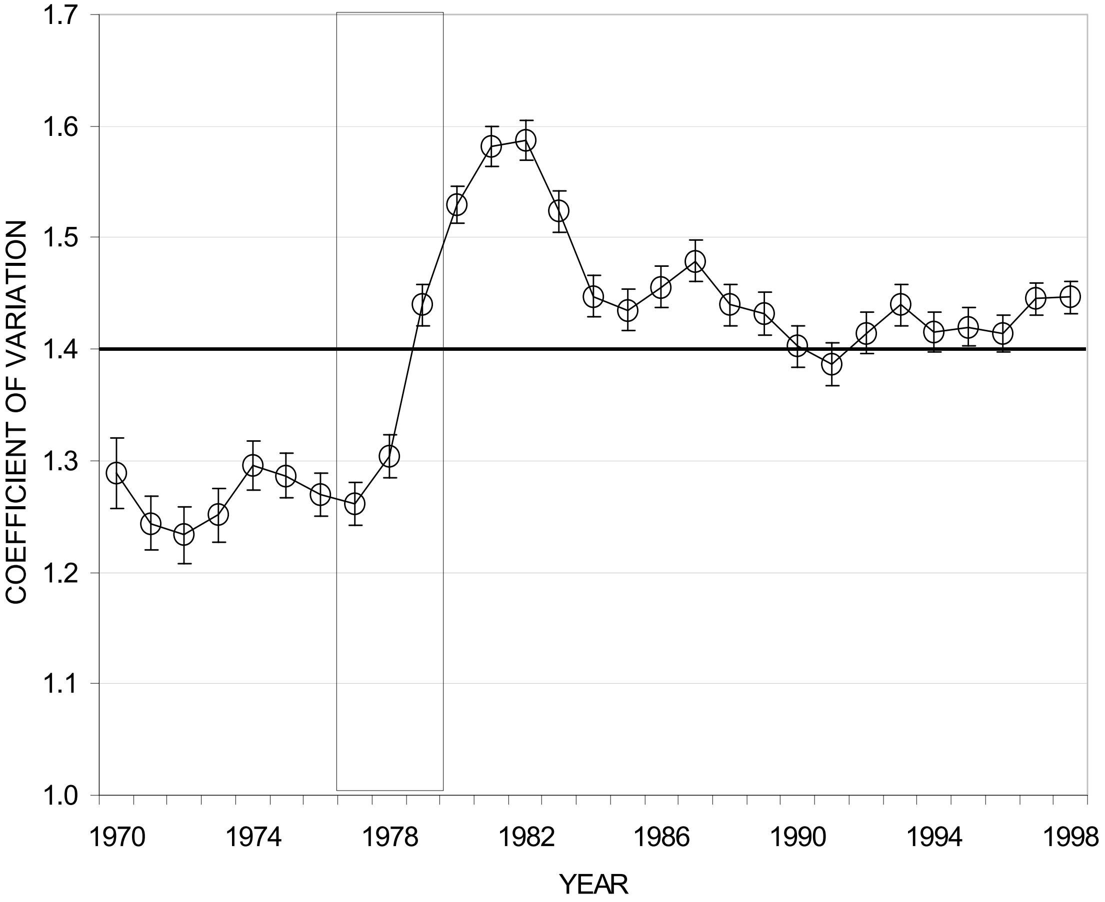


Figure 5.1. Coefficient of variation (CV) (±SE) in annual North American Breeding Bird Survey counts of Northern Bobwhite in Illinois. The black line at CV = 1.4 denotes the mean CV over the period. The vertical rectangle denotes a period of severe winters in the late-1970s (Chapter 6).

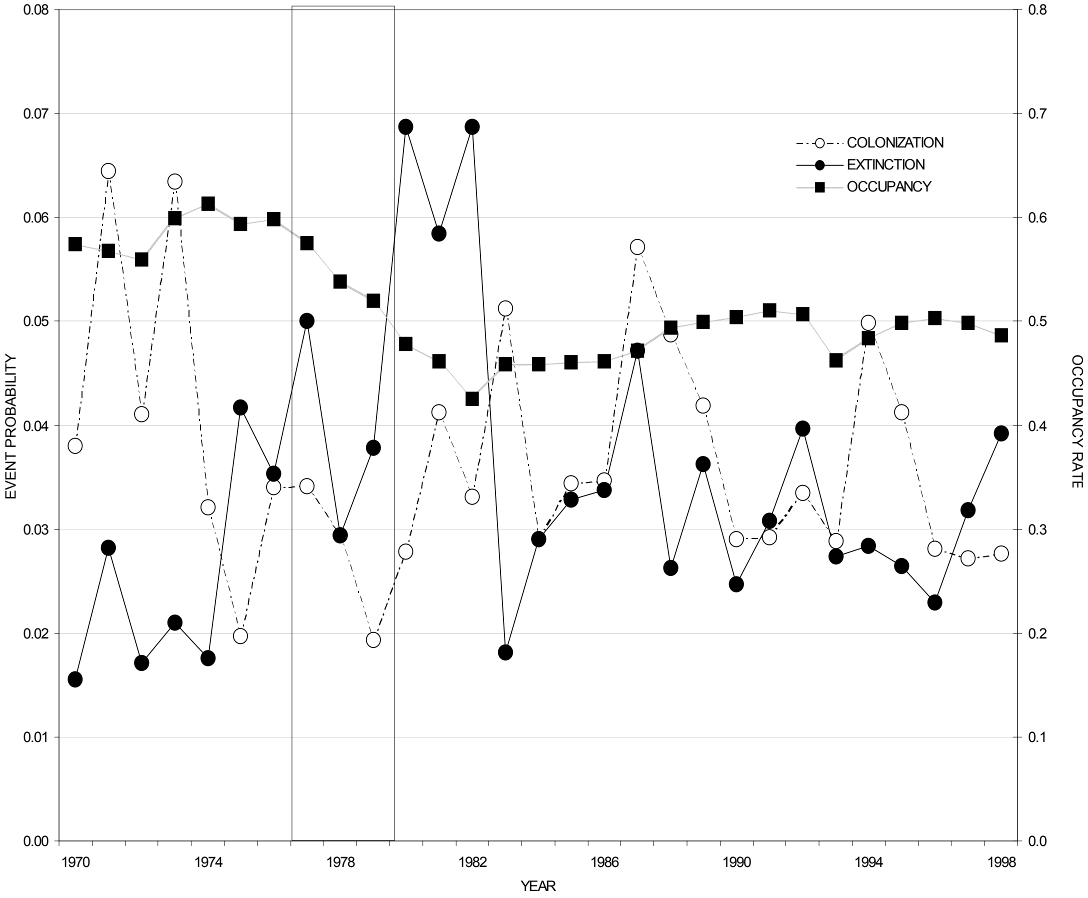


Figure 5.2. Observed annual extinction, colonization, and occupancy rates for Northern Bobwhite at North American Breeding Bird Survey locations in Illinois. The vertical rectangle denotes a period of severe winters in the late-1970s (Chapter 6).

extinction. The single route maintaining a population was recolonized only 2 yrs after initial extirpation.

Probability of persistence for 100 years was calculated as:

$$(1\text{-Pr(Ext)} + \text{Pr(Col)})^{100}. \qquad \text{(Equation 5.6)}$$

Given that probability of extirpation exceeded colonization for bobwhite measured at IDNR stop locations, mean probability of persistence for 100 years was only 0.0129. This translated, after trigonometric modification of Eqn. 5.4, to $T_{qe} = 23$ yrs.

Modeling Approach

Population indices from 59 NABBS and 50 IDNR routes were evaluated (Table 5.1, Appendices 5.A, 5.B). The model performed as expected, predicting T_{qe} as a function of mean index of abundance, variance in the rate of change (V_r), and the degree of temporal autocorrelation (Fig. 5.4). Model output suggested a non-linear relationship between V_r and T_e (Fig. 5.5). Only populations exhibiting a very low V_r produced a time to extinction beyond the foreseeable future.

The serial correlation coefficient for the 2 data sets, state-wide NABBS and quail-range IDNR, indicated diverse patterns in dynamics (Table 5.1). State-wide quail populations were effected only by environmental factors (sensu Foley 1994) in the current year ($\bar{x}_\rho = -0.363 \pm 0.026$), whereas within the quail range, bobwhite populations exhibited some carry over in their effect on year to year abundance ($\bar{x}_\rho = 0.345 \pm 0.044$).

Persistence Probability.—Mean probability of persistence for 100 yrs for state-wide estimates (i.e., NABBS data) of individual bobwhite populations was 0.223 ± 0.034

Table 5.1. Mean model parameter estimates for extinction models derived from North American Breeding Bird Survey and Illinois Department of Natural Resources call counts of Northern Bobwhite. Population rate of change is denoted by *r*, ρ is the serial autocorrelation of environmental effects, V is the variance in population rate of growth when $r = 0$ and $r \neq 0$, respectively, T_e is time to extinction, and *P*(t) is the likelihood of extinction within the next century.

	Data set	*r*	ρ	V_r	V_{re}	T_e	*P*(t)
Mean	NABBS	0.02	-0.36	0.69	0.32	96.8	0.223
SE		0.01	0.03	0.08	0.04	16.4	0.035
Min		-0.27	-0.83	0.05	0.02	0	0
Max		0.44	0.05	2.65	1.11	721.4	0.871
Mean	IDNR	0.04	0.34	1.55	4.15	73.24	0.15
SE		0.15	0.31	1.38	5.47	51.83	0.20
Min		-0.27	-0.62	0.23	0.09	3.09	0
Max		0.69	0.80	5.47	26.25	1,051.3	0.91

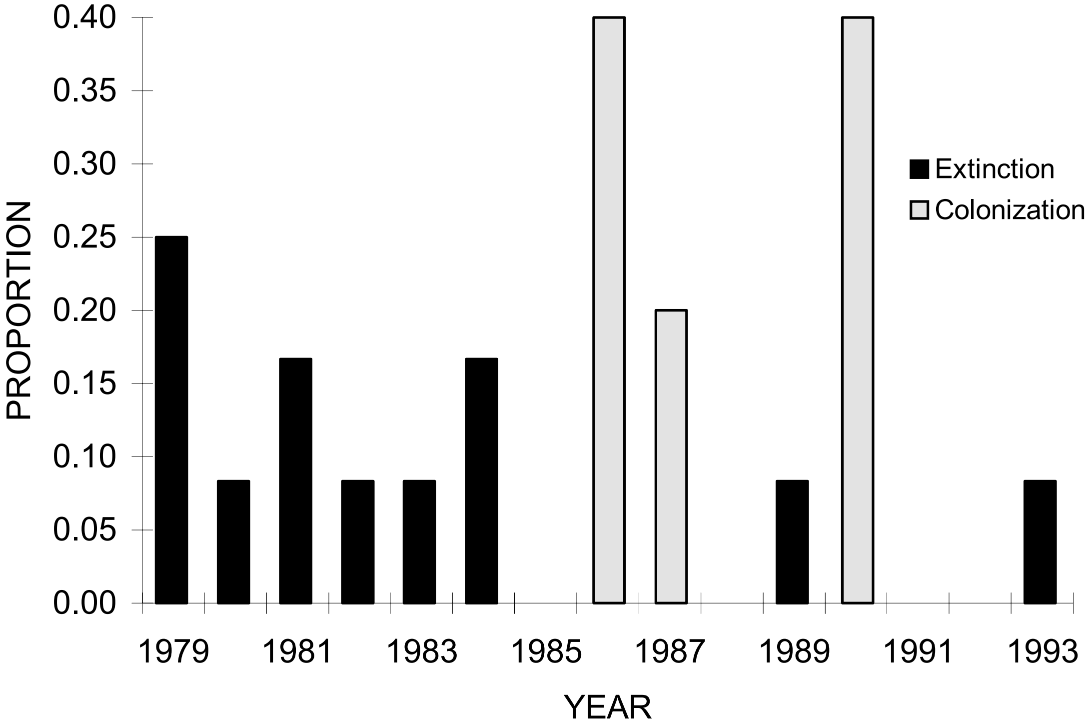


Figure 5.3. Frequency of extinction and recolonization events in Northern Bobwhite of Illinois, as determined from North American Breeding Bird Survey call counts.

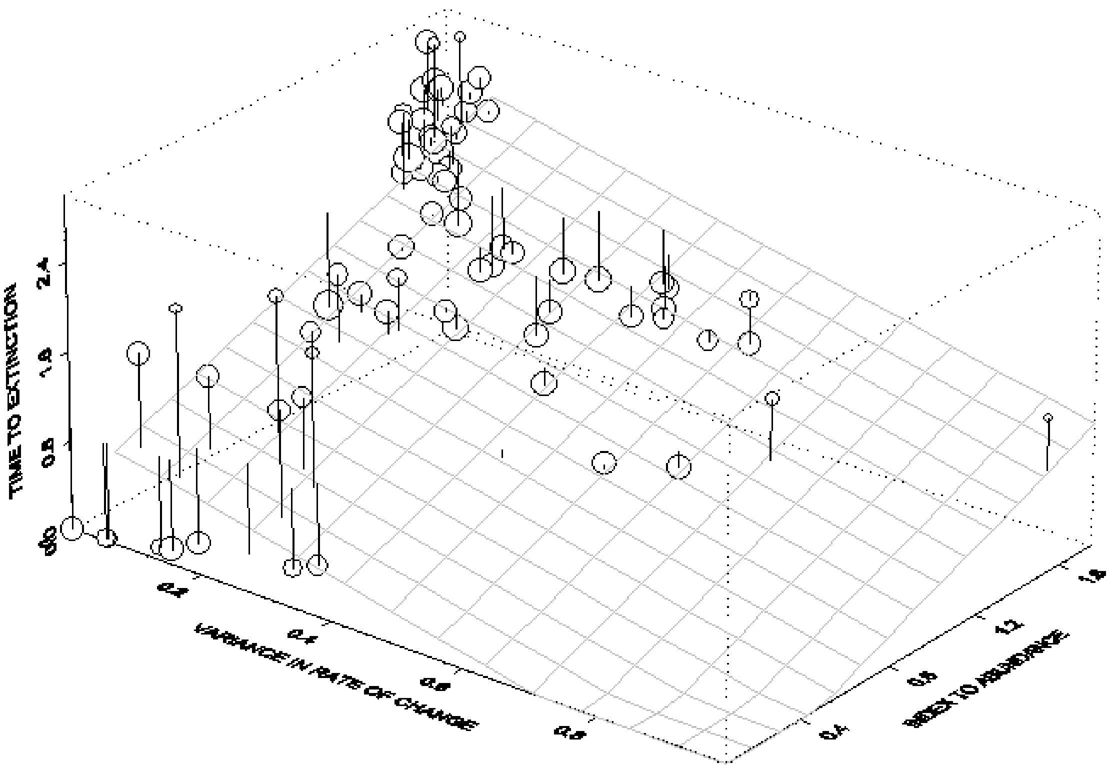


Figure 5.4. Time to quasi-extinction for Northern Bobwhite in Illinois as a multivariate non-linear function of mean index to abundance, variance in population rate of change, and the temporal autocorrelation. Bubble size varies as a function of temporal first-order autocorrelation, and the lines denote the distance of the bubble from the time to extinction surface. Data are from North American Breeding Bird Survey counts; plots based on Illinois Department of Natural Resources call counts are similar.

(*n* = 59, range = 0.000–0.871), whereas populations measured by IDNR specifically within the quail range exhibited a mean persistence probability of 0.155 ± 0.028 (*n* = 50, range = 0.000–0.909). A Mann-Whitney test indicated this apparent difference between persistence probability of the 2 data sets was not real (U = 0.12, *P* = 0.90).

Times to Extinction.—Mean time to extinction for state-wide estimates of individual populations was 96.8 ± 16.4 (*n* = 59, range = 0–721 yrs). Within the quail range, IDNR data suggested mean T_{qe} was 73.2 ± 21.5 (*n* = 50, range = 3.1–1,051.3 yrs) (Fig. 5.6). Again, a Mann-Whitney test indicated no difference in the 2 data sets (U = -0.27, *P* = 0.78). Quail populations throughout most of the historical quail range were predicted to persist beyond 100 years (Fig. 5.7). The populations most secure appeared to reside in Fulton, Jasper, and Macon Counties.

For those counts predicted to equal 0 by 1998, I examined route abundance in each year from 1997–2000 (Table 5.2). The model appeared to predict NABBS data better than IDNR data. Three of 9 NABBS routes exhibited 0 counts in the predicted year of extirpation; 2 other routes produced counts ≤ 6. However, either due to uncounted residents or immigrants from neighboring habitat, counts in subsequent years fluctuated around 0 for 2 routes; only 1 route, New Lenox, actually exhibited permanent extinction of the population. As mentioned in the previous section (Empirical Assessment), none of the IDNR routes proceeded to extinction. None of the 12 routes predicted by the model proceeded to extinction and only 5 of 12 route counts were even below the long-term mean.

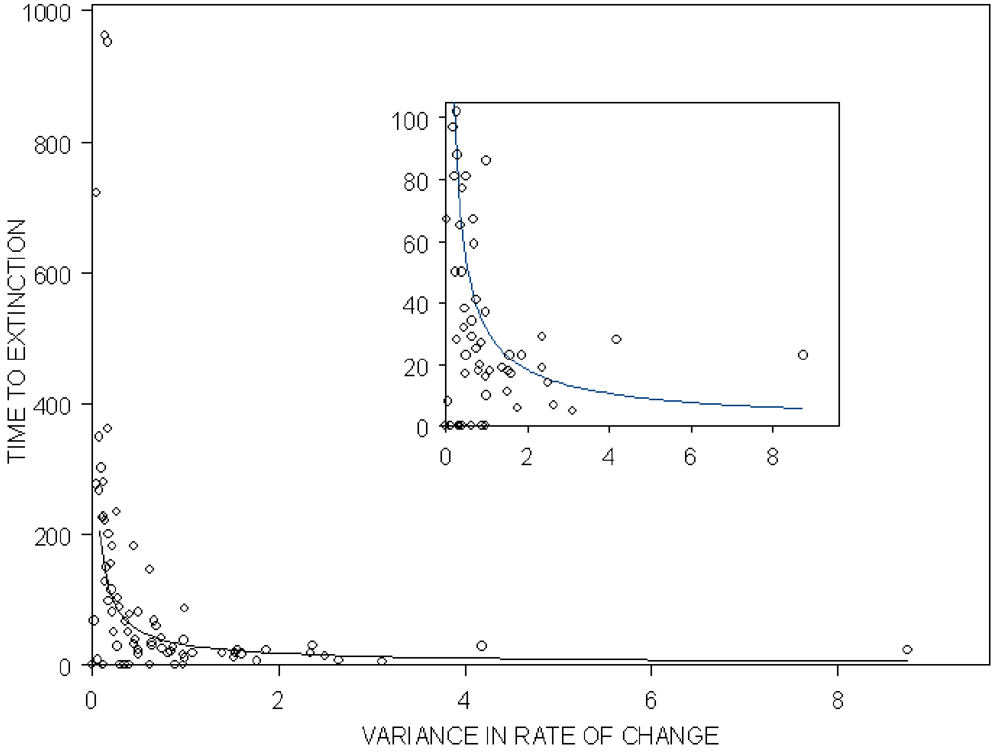


Figure 5.5. Time to quasi-extinction for Northern Bobwhite in Illinois as a function of variance in the rate of change.

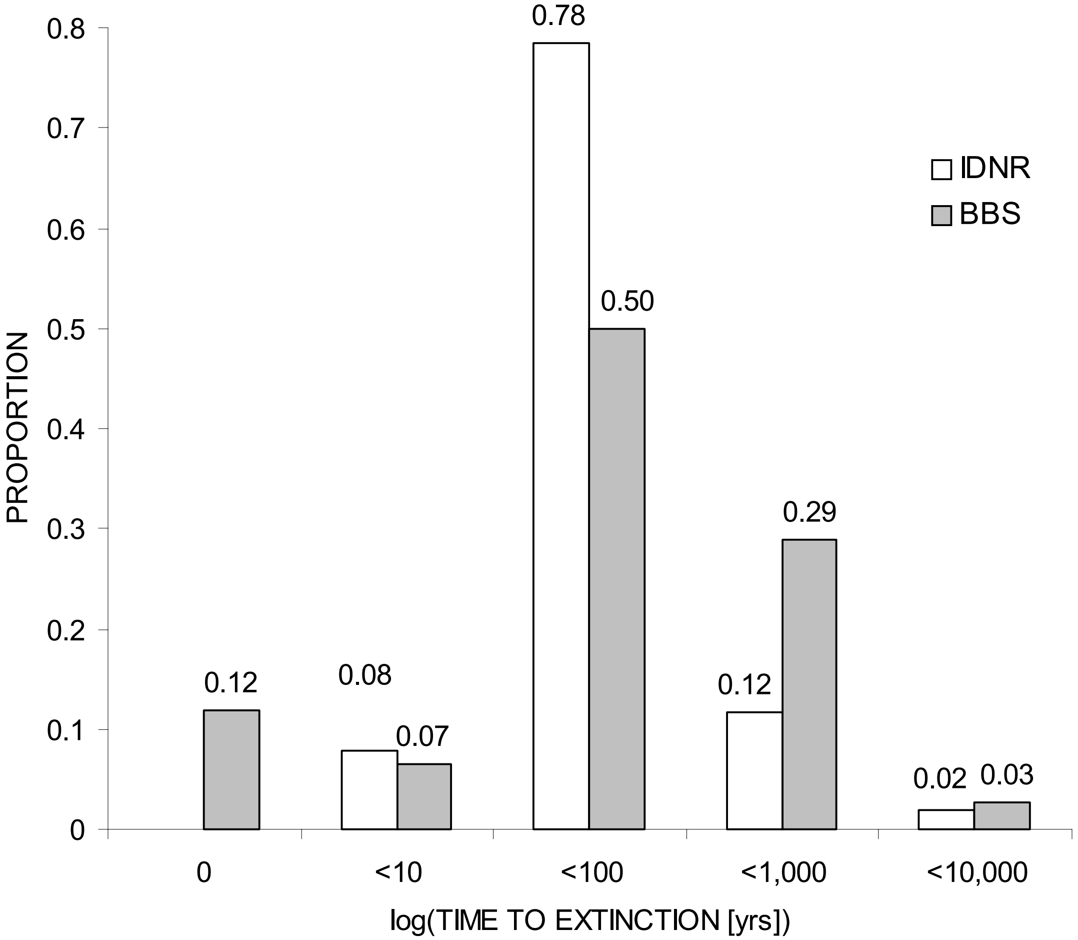


Figure 5.6. Time to quasi-extinction for Northern Bobwhite populations in Illinois as determined for Illinois Department of Natural Resources (IDNR) and North American Breeding Bird Survey (BBS) routes, 1981–1998.

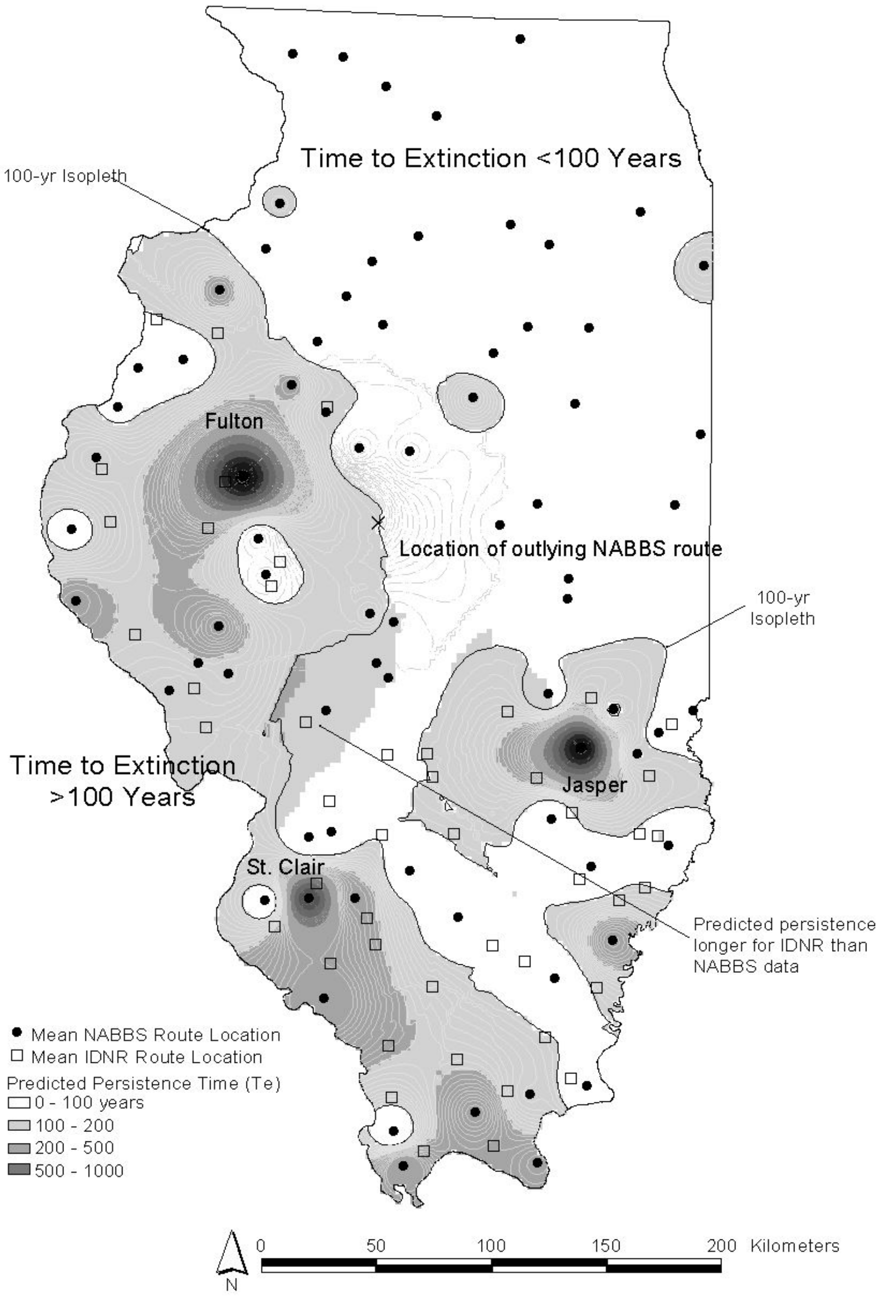


Figure 5.7. Geographical extent of predicted times to quasi-extinction for Northern Bobwhite in Illinois. Data were interpolated by inverse distance weighting of information from 12 neighboring survey locations, with 1 outlier removed from the NABBS interpolation. Contours are at 100-yr intervals.

Table 5.2. Comparison of counts of Northern Bobwhite predicted to be extinct by 1998 and results of counts conducted from 1997–2000. NR indicates the route was not run; NA indicates the data were not available.

Route (No.)	Data Set	Predicted Year of Extirpation	Total counts in yr previous, year of predicted extirpation, and 2 years following[‡]
Guilford (1)	BBS	1998	5/6/7/3
Putnam (9)	BBS	1998	NR/27/9/24
Buda (11)	BBS	1992	10/13/14/40
New Lenox (18)	BBS	1986	NR[*]/0/NR/0
Terre Haute (22)	BBS	1998	12/22/13/17
Monticello (30)	BBS	1982	0[@]/0/2/0
Dailey (33)	BBS	1993	0/14/8/25
Milford (34)	BBS	1982	4/0/2/0
Mt. Vernon (55)	BBS	2000	49/51/NA/NA

Table 5.2. Continued.

Route (No.)	Data Set	Predicted Year of Extirpation	Total counts in yr previous, year of predicted extirpation, and 2 years following‡
Adams	IDNR	1998	299/362/192/NA
Cass	IDNR	1983	70#/137/46#/78
Gallatin/Hardin	IDNR	1984	333/233/225/94#
Montgomery	IDNR	2000	76/NA/NA/NA
Perry	IDNR	1991	383/393/262/259
Pope/Johnson	IDNR	2002	NA/NA/NA/NA
Saline	IDNR	1984	435/274/550/302^
St. Clair	IDNR	2000	170/NA/NA/NA
Union	IDNR	1994	74/110/89/20#
Wabash	IDNR	1991	210/202/320/158

Table 5.2. Continued.

Route (No.)	Data Set	Predicted Year of Extirpation	Total counts in yr previous, year of predicted extirpation, and 2 years following[‡]
Warren	IDNR	2001	NA/NA/NA/NA
Wayne	IDNR	1998	145/121/94/NA
Williamson	IDNR	1990	97[#]/52[#]/52[#]/86

[‡] NR, route was not run that year.
[*] 1 the previous year.
[@] Proceeded to extinction ca. 1978.
[#] Bobwhite missing from >40% of stops.
^ In 1998, index down to 52, with bobwhite present at only 32% of sites, down from 100%.

Variance in r.—Areas with the highest variance in relation to intrinsic population growth, sites at-risk of extirpation due to environmental stochasticity, occurred primarily in southeastern Illinois. Variance in r was related to mean abundance in each data set (Table 5.3). Variance was related to mean abundance in a curvilinear fashion for the state-wide NABBS data, and in a negative linear fashion for quail-range IDNR data. In neither case did b exceed 1, indicating stable population dynamics following May's (1974) criterion.

DISCUSSION

I expressed the population-dynamic process as a Markovian transition model in which population size fluctuated as a density-dependent population process modified by (environmental and demographic) stochasticity. The model I used integrated population rate of change and variance in population rate of change to model extirpation probabilities. A population may be extirpated when 1) mean rate of change is negative (deterministic extinction) or 2) population variance is too great (demographic stochasticity).

Extinction risk was positively associated with variation in population rate of change, likely due to positive associations between variance in abundance and extinction risk (Karr 1982, Pimm et al. 1988, Vucetich et al. 2000). Mean variation in indices of bobwhite abundance were 3–4 times greater for bobwhite than those found in a review of counts of small- ($\bar{x}_{CV} = 0.57$, range = 0.11–2.48) and large- ($\bar{x}_{CV} = 0.36$) bodied birds (Gibbs 2000). Variance in bobwhite rate of change (mean $V_r = 0.82$, median = 0.43), as measured by BBS counts, was intermediate to insect ($V_r \approx 0.84$ to 1.46) and large mammal

Table 5.3. Least-squares estimates of the relationship between variance in the rate of change and mean abundance of Northern Bobwhite populations in Illinois since 1980.

Parameter	Estimate (SE)	*t*	*P*
NABBS			
Intercept	-0.0849 (0.0485)	-1.75	0.085
log(Mean Abundance)	0.2465 (0.0946)	2.61	0.012
log(Mean Abundance)^2	-0.2222 (0.0680)	-3.29	0.002
IDNR			
Intercept	0.9360 (0.2764)	3.39	0.001
log(Mean Abundance)	-0.3932 (0.1189)	-3.31	0.002

populations ($V_r = 0.01$) and similar to other bird populations (Foley 1997). Model results suggested only those populations with a $V_r \leq \overline{V_r}$ possessed a time to extinction beyond the near future, indicating extinctions are a common risk for greater than half the Illinois bobwhite populations (the half possessing $V_r \geq \overline{V_r}$).

Variation in midwestern bobwhite population dynamics is generally attributed to winter mortality and the effects winter weather has on subsequent reproduction (Chapter6). Roseberry and Klimstra (1984) demonstrated bobwhite abundance in Illinois may fluctuate as much as 300% between years, and that these fluctuations were due to density-dependent responses of bobwhite to past levels of snowfall. In 1978 and 1979, when annual snowfall was twice as great as the long-term mean, bobwhite were decimated in Illinois, causing a contraction in the species' Illinois range and a lowering of abundance state-wide (Chapter 6). Catastrophes such as these severe winters heighten extirpation probabilities. They also resulted in heightened colonization probabilities as well, probably because empty habitat was still suitable for re-occupation. However, even after typical winter weather conditions resumed post-1980, subsequent estimates of CV were elevated by ~13% over pre-1980 estimates and continue to be elevated today.

Differences in CV between bobwhite and most other avian species emphasizes the relative dynamic variability of bobwhite populations. Only 10 other avian populations summarized by Gibbs (2000) possessed similar or larger CVs (Table 5.4). Most of the European species from Hogstad's (1993) study were common residents of woodland/agriculture edge, as bobwhite are. There appear to be no other similarities to

Table 5.4. Coefficients of variation estimated for local populations of avian species. Except for 3 larger-bodied galliforms included for comparison, only non-galliform species with coefficients similar to Northern Bobwhite were included.

Species	Length of time series	CV	Source
Ring-necked pheasant (*Phasianus colchicus*)	5	0.35	Pimm et al. (1988)
Red Grouse (*Lagopus l. scoticus*)	5	0.44	Lack (1969)
Gray Partridge (*Perdix perdix*)	5	0.68	Pimm et al. (1988)
Dark-eyed Junco (*Junco hyemalis*)	17	1.15	Holmes and Sherry (1988)
Lesser Whitethroat (*Sylvia curruca*)	12	1.23	Hogstad (1993)
Greenfinch (*Carduelis chloris*)	12	1.23	Hogstad (1993)
Capinera (*Sylvia atricapilla*)	12	1.32	Hogstad (1993)

Table 5.4. Continued.

Species	Length of time series	CV	Source
Northern Bobwhite (*Colinus virginianus*)	29	1.40	This study
Winter Wren (*Troglodytes troglodytes*)	17	1.45	Holmes and Sherry (1988)
Common Magpie (*Pica pica*)	12	1.49	Hogstad (1993)
Garden Warbler (*Sylvia borin*)	12	1.81	Hogstad (1993)
Long-tailed Tit (*Aegithalos caudatus*)	12	2.33	Hogstad (1993)
Spotted Flycatcher (*Muscicapa striata*)	12	2.48	Hogstad (1993)

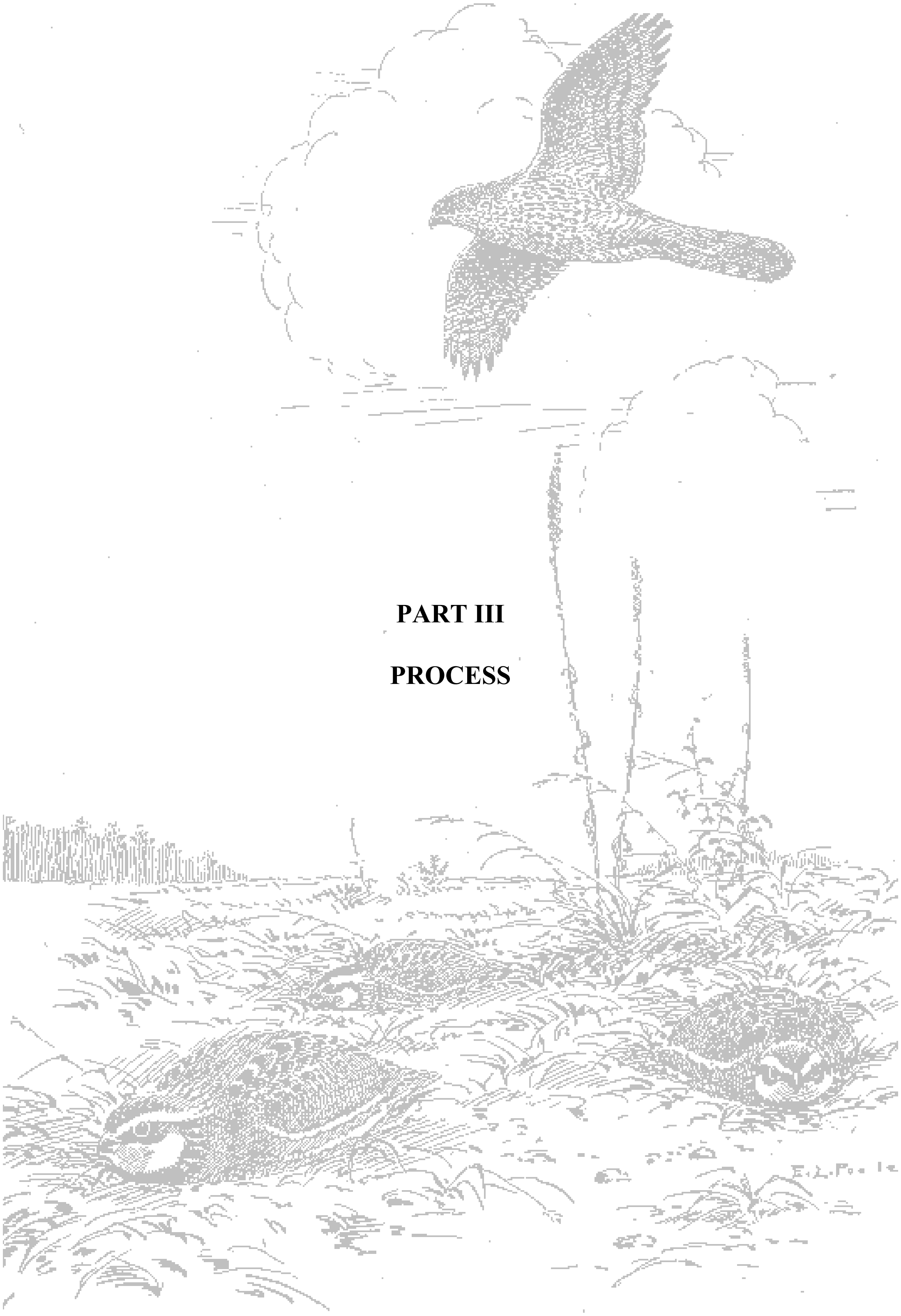
explain why these various species exhibit such large variation. It may be due, in some part, to their patchy distribution across the landscape; a patchy distribution for a mobile species would lead to large annual variability in counts if the counts were taken at a point location. This is not likely to be the case with bobwhite, in that bobwhite are quite sedentary and generally occupy home ranges ($\ll$30 ha) smaller than the size of the listening circle (50 ha). Thus, a point count should accurately measure annual biological response for bobwhite around the point location if population extirpation is not high. Alternatively, it may be that this increased variability is simply a reflection of past population disturbances, and species occupying farmland/woodland landscapes may be at greater risk of perturbation, thus reflecting this in a heightened CV.

State Transition.—Despite May's (1974) suggestion that variability in population dynamics may contribute to population extirpation, extirpations in Illinois did not seem to be directly linked to variability in bobwhite abundance. Observed annual state transition probabilities ($Pr_{extinction} = 0.13$, $Pr_{colonization} = 0.09$) were comparatively low, suggesting bobwhite in Illinois occur in a fairly static system, despite their variability, at least within the time frame I analyzed.

Extirpations after 1980 appeared to be a continued relaxation of populations after the severe winters of the late 1970s (Chapter 6). Colonizations were observed only in 1986, 1987, and 1990, 3 years in which total winter snowfall was 20% below the long-term mean. Thus, years with low snowfall may facilitate occupation of habitat by increasing survival of immigrants occupying novel habitat.

Times to Extirpation.—Brennan (1991) predicted extirpation of bobwhite to unharvestable levels by 2000 and complete extirpation by 2025. For Illinois, this is a pessimistic prediction. Extrapolating empirical transition probabilities, which include transitions heightened by the severe winters of the late-1970s, indicates half of the populations will persist beyond 2020. Model predictions, based on data from the recent stationary period, indicates half of the populations will persist beyond 2070, and possibly much longer. If populations in Illinois are not buffeted by additional episodes of severe weather and stationarity of abundance can be maintained, bobwhite should persist for several more generations of hunters.

Effects of global warming will reduce the severity of future winter weather in Illinois (Easterling et al. 2000; Chapter 10:215); thus, bobwhite are less likely to see a repeat of the severe winters of the late-1970s. However, given uncertainty in climate predictions (for instance, might probability of drought increase?), it is premature to suggest future weather conditions will not negatively influence population persistence. In addition, continued anthropogenic alteration of the landscape (Chapter 2) will likely prevent continued stationarity in abundance. Should urbanization, reforestation, and large-scale agriculture increase in abundance at a rate greater than increases in set-aside programs such as the Conservation Reserve Program, it is easy to imagine bobwhite extinction in Illinois occurring sooner than envisioned.



PART III

PROCESS

CHAPTER SIX

INFLUENCE OF CLIMATE ON BOBWHITE DISTRIBUTION AND ABUNDANCE: EFFECTS OF REGIONAL AND GLOBAL WEATHER PHENOMENA

> *Climate plays an important part in determining the average number*
> *of a species, and periodical seasons of extreme cold or drought,*
> *I believe to be the most effective of all checks.*
> Charles Darwin (in the *Origin of Species*)

The study of climatological conditions on biological response in Northern Bobwhite has been a lengthy one. For bobwhite in the southern portion of its range, major fluctuations in abundance (Chapter 3) are attributed to effects of water deprivation or drought (Kiel 1976, Cain and Lien 1985, Koerth and Guthery 1991, Bridges et al. 2001; however, see Giuliano and Lutz 1993 for contrary evidence for effects of drought). In northern portions of the species range, severe winter weather affects quail populations by increasing winter mortality (Mosby and Overton 1950, Kozicky and Hendrickson 1952, Roseberry 1962, Kabat and Thompson 1963, Stanford 1972) and reducing productivity the following spring and summer (Edwards 1972, Roseberry and Klimstra 1972, Stanford 1972, Roseberry et al. 1979).

Snowfall is the primary correlate to quail mortality in the central US (Errington 1945, Roseberry 1962, Kabat and Thompson 1963). Kozicky and Hendrickson (1952) reported a significant correlation between winter losses and snow depth in Iowa, with losses ranging from 20–88%. Kabat and Thompson (1963:3) found winter mortality was directly correlated with the number of months in which snow depths exceeded 7.5 cm. Based simply on winter weather conditions, Kabat and Thompson (1963) believed the percentage of bobwhite succumbing to winter mortality could be predicted within ±15%.

While effects of local climate perturbations on individuals and populations are well-established, less well known are effects of regional and global climatological conditions on bobwhite abundance and distribution. Investigations into the ecological implications of large-scale climatic processes are critical for predicting potential consequences of climate change to quail abundance (Post et al. 1999, Guthery et al. 2001*a*).

I examined influences of regional and global weather conditions on state-wide bobwhite population dynamics by conducting a multivariate time-series analyses, whereby various time series of climatological variables were related to time series of Northern Bobwhite abundance. Based on previous published findings, I focused a spatially-explicit state-wide examination on variables related to winter severity. Because weather events in spring are often carried over from the previous winter and have the potential to negatively influence reproduction in bobwhite, I also examined various spring temperature and precipitation variables. Additionally, I assessed effects of annual drought conditions on bobwhite abundance to provide a northerly perspective. Recently, Bridges (1999) and Bridges et al. (2001) reported significant negative associations between bobwhite abundance and drought severity in Texas. Roseberry (1989), who provided a thorough review of this topic, believed drought adversely affected quail reproduction and subsequent fall abundance in southern Illinois based on analyses of a

39-yr time series of

bobwhite population and weather data.

Global Climate Processes

Regional or state-wide weather events are a product of large-scale weather phenomena. An understanding of how global climate processes influence regional bobwhite abundance is clearly a necessity given increasing global temperatures, ozone depletion, atmospheric pollution, and other anthropogenic assaults on the atmosphere and associated climate patterns (Davis et al. 1998, Spurgeon 2000). Several global weather indices were examined: the El Niño Southern Oscillation, Pacific Decadal Oscillation, Arctic Oscillation, and North Atlantic Oscillation.

El Niño Southern Oscillation.—The well-known El Niño Southern Oscillation (ENSO) is a combination of interannual fluctuations in tropical sea level pressure coupled with irregularly occurring episodes of heightened sea surface temperature in the eastern Pacific (Trenberth 1997). El Niño (EN) is a relaxation in trade winds in the central and western Pacific leading to a depression in the thermocline in the eastern Pacific and a rise in the thermocline in the west (Philander 1990). This reduces upwelling of cool water to the surface, resulting in a rise in sea surface temperature. El Niño events occur irregularly at intervals of 2–7 years, although the average is about once every 3–4 years; they persist for 12–18 months. El Niño events describe the *warm* phase of ENSO, whereas La Niña describes the *cool* phase. Accompanying El Niño are swings in the Southern Oscillation (SO), an interannual fluctuation in tropical sea level pressure between the eastern and western hemispheres. Large changes in global atmospheric circulation result as a consequence of the combined El Niño and Southern Oscillation (ENSO), forcing changes in weather in regions far removed from the tropical Pacific. Impacts of ENSO upon climate in temperate latitudes are most evident during wintertime. For example, most El Niño winters are mild over western Canada and parts of the northern United States, and wet over the southern United States from Texas to Florida. In Illinois, corn yield is either adversely (*cool* phase) or positively (*warm* phase) impacted (Mauget and Upchurch 1999); the cool phase of ENSO is also associated with an increase in the number of tornadoes in Illinois (Bove, *In press*).

Pacific Decadal Oscillation.—The Pacific Decadal Oscillation (PDO) is similar to ENSO in that it too is a long-lived pattern in Pacific climate variability (Latif and Barnett 1994). However, it is distinguished from ENSO by being a longer phenomenon, persisting 20–30 years, and the climatic fingerprints of PDO are most visible in the North Pacific/North American sector with only secondary signatures in the tropics (just the opposite for ENSO). There appear to be only 2 full PDO cycles in the past century: *cool* PDO regimes prevailing from 1890–1924 and again from 1947–1976, whereas *warm* PDO regimes occurred from 1925–1946 and from 1977 to the mid-1990's (Minobe 1999). In Illinois, October–March precipitation is reduced during the warm phase PDO and increased during the cool phase PDO (Mantua, *In press*). Bove (1999) and others have reported linkages between PDO and ENSO.

Arctic Oscillation.—The Arctic Oscillation (AO) involves a counterclockwise spinning ring of air encircling the polar region (Cutlip 2000). Unlike ENSO and PDO, which are driven by sea-surface temperature shifts in the Pacific, the AO appears driven by processes in the stratosphere (Kerr 1999). Fluctuations in the oscillation create a seesaw pattern in which atmospheric pressure at polar and middle latitudes alternate between positive and negative phases. A negative phase brings higher-than-normal pressure over the polar region and lower-than-normal pressure at about 45° north latitude, bringing more cold outbreaks and snowy weather to the US east of the Rocky Mountains. A positive phase brings the opposite conditions, steering ocean storms farther north and bringing milder conditions to the eastern US. In recent years, the Arctic Oscillation has been mostly in its positive phase.

North Atlantic Oscillation.—A well known index, the North Atlantic Oscillation (NAO) index (Hurrell 1996, Hurrell et al. 2001), is closely related to AO (Kerr 1999). The NAO is a meridional oscillation in atmospheric mass over the North Atlantic. It fluctuates on interannual and decadal time scales (Hurrell 1995, 1996). The NAO determines as much as 33% of the interannual variation in winter precipitation (Hurrell 1996) and up to 55% of the interannual variation in mean temperature in the Northern Hemisphere (Schlesinger and Ramankutty 1994). When NAO is in its *low* state, warm temperatures and precipitation remain over North America, whereas when in its *high* state, strong westerly winds push the warm air and precipitation over Europe. For North America, particularly the eastern half, low values are associated with warm, wet winters and high values are associated with cold, dry winters.

Nodal Lunar Cycle.— While not directly a global climate process, I also assessed the potential influence of the nodal lunar cycle because Roseberry and Klimstra (1984) believed the nodal lunar cycle was correlated with bobwhite abundance. The lunar nodal cycle is the time required (18.6134 years) for the line formed by intersection of the Moon's orbital plane and the plane of the Earth's orbit (= lunar node) to rotate through 360°. The lunar-nodal cycle appears to affect many environmental factors, including atmospheric pressure, precipitation, atmospheric dust, timing and height of tides, and extent of moon light (Kaye and Stuckey 1973; Archibald 1977; Currie 1987, 1994; Currie et al. 1993). Parker et al. (1995) demonstrated a relationship between periodicity in an index of recruitment of Pacific halibut (*Hippoglossus stenolepis*) and the nearly identical period of the 18.6-yr lunar nodal cycle. They were, however, unable to provide a mechanism whereby such a minor physical effect could produce such pronounced changes, but they suggested some sort of systemic amplification was likely at work.

Since overwinter survival of bobwhite is principally a function of winter severity, discerning patterns in annual climatological conditions may be useful in understanding bobwhite abundance. Knowing what we do about the proximate causes of adverse weather conditions on bobwhite abundance, my first objective was to examine the regional influences of adverse meteorological conditions on historical levels of bobwhite abundance. Bobwhite are less abundant in the northern portion of the state despite the presence of seemingly suitable habitat. I examined whether historical patterns in climate could explain bobwhite distribution. Graber and Graber (1979, 1983) and Norris and Elder (1982) noted the negative effects of winters in the late-1970s on avian abundance in Illinois and Missouri. Thus, due to these severe winters and a coincident drop in bobwhite indices, I concentrated my analyses on the late-1970s (Fig. 6.1).

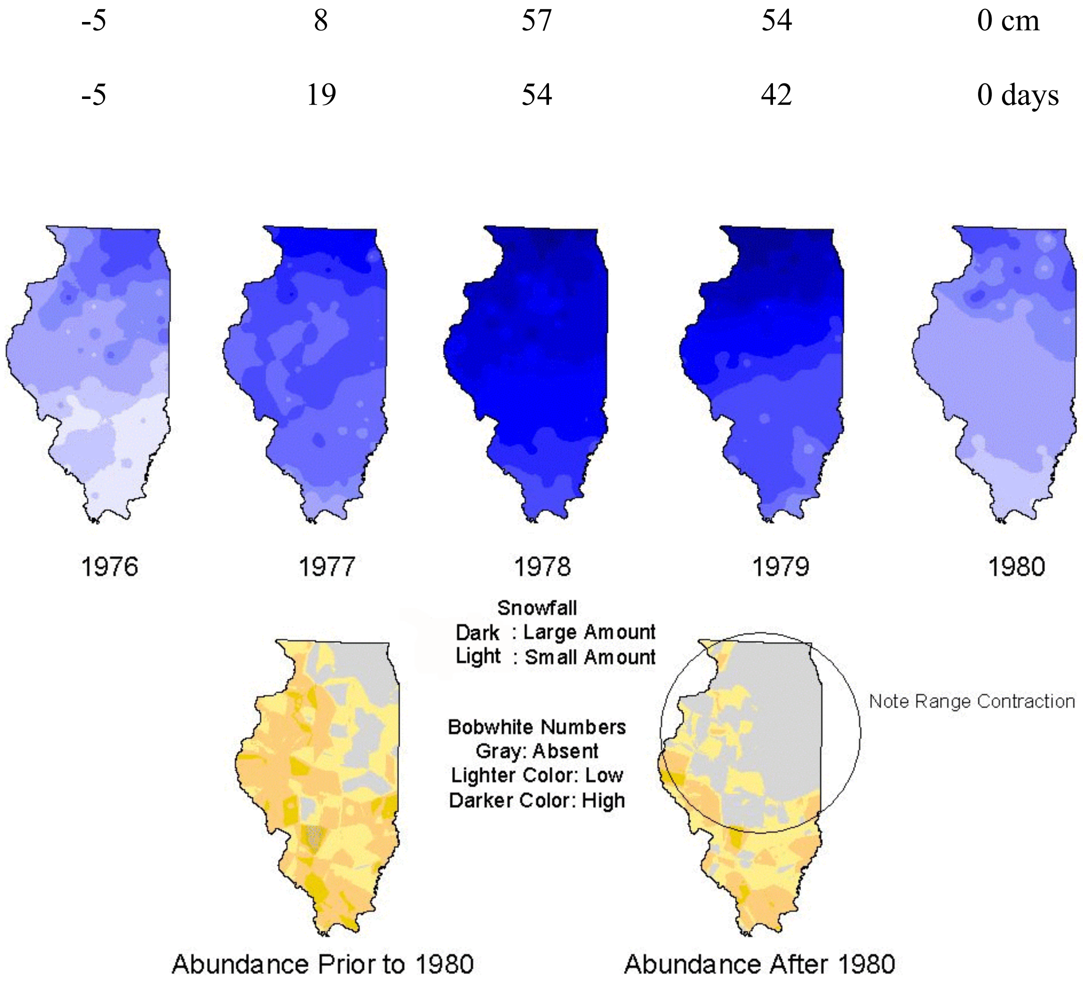


Figure 6.1. Bobwhite abundance and distribution retracted considerably in the late-1970s, probably due to a series of severe winters. Annual amount and number of days of snow above the 30-yr mean are noted above each panel.

METHODS

Regional Weather Phenomena

Monthly surface weather data were downloaded from the National Climatic Data Center webpage (Http://www.ncdc.noaa.gov). Latitude and Longitude (Geographic Reference System) for each weather station in Illinois were reprojected to Eastings and Northings (Universal Transverse Mercator projection) with the *project* command in Arc/INFO (Environmental Systems Research Institute, Redlands, California, USA).

Climatic data were linked to weather station location data with various queries conducted in the relational database MSAccess (Microsoft Corp., Seattle, Washington, USA). Values for number of winter days with snow coverage ≥2.54 cm, total winter snow depth (cm), mean spring temperature (°C), mean spring precipitation (cm), and coefficients of variation in monthly spring temperature and precipitation were derived from monthly summaries. Snow variables were derived for the Oct–Mar interval (for temperature and other precipitation variables winter was defined as Dec–Feb), whereas spring was defined as Mar–May.

Variables were interpolated state-wide for each year between 1966 and 1998. The *inverse distance weighted* procedure (IDW; Isaaks and Srivastava 1989) in the Spatial Analyst extension of ArcView was used to interpolate values between weather stations. The IDW procedure interpolates areas of unknown value based on proximity to points of known value; points closer are weighted more heavily than those farther away. Use of IDW assumes the influence of the known location on the interpolated value decreases with distance from the sampled location; the slope of the decline is dictated by values at neighboring known points. The IDW interpolation is suitable for Illinois climatological data since Illinois is relatively flat ($\bar{x}_{\text{slope}} < 1°$) and has an extensive and thoroughly distributed set of weather stations (J. Angel, Illinois State Climatologist, personal communication).

To maintain consistency between interpolation grids, output grid size was arbitrarily set at 250 × 250 m (6.25 ha), and number of rows and columns was set to 2,723 and 4,487, respectively. Number of neighbors used in the interpolations was set to 12 and a 2° power function was used. The interpolated grids represent regionalized weather patterns, justifying use of the rather large cell size. Interpolation grids were visually assessed to insure rarity of "holes" (areas of obvious inadequate interpolation).

Local variation in weather was not represented by the interpolation scheme that I chose because inverse distance weighting with a 2° power function results in a smoothing of the variable over a neighborhood of 12 stations. This smoothing removes extreme weather events occurring in a local area smaller than the neighborhood being used to calculate the interpolations. Capturing this local variation in weather is beyond the scope of this investigation.

Bridges (1999) and Bridges et al. (2001) indicated the best index to measure severity of drought was the Modified Palmer Drought Severity Index (MPDSI; Alley 1984). The MPDSI simultaneously scales precipitation, average temperature, water holding capacities of soil, and evapo-transpiration. I acquired and georeferenced monthly calculations of MPDSI from the NCDC webpage for the 9 weather divisions in Illinois for the period 1966–1998. These monthly calculations were summed to provide an annual index of long-term drought severity. The NCDC re-scales the annual index by dividing by 12, and in doing so creates a mean drought severity for the year. I retained the sum, rather than the mean, of the monthly indices for initial analysis.

Annual climate parameters were related to quail abundance only spatially and not temporally. I did not assess influence of regional weather conditions on serial quail abundance because such an approach is currently unwieldy given >4,000 spatial locations and because complete time series of abundance for each location were not available over sufficient space as to make the analysis unfeasible.

Global Weather Phenomena

Four indices of monthly global weather phenomena, PDO, ENSO, AO, NAO, were downloaded from various internet locations (Table 6.1). The Lunar Nodal Cycle was determined by tallying the minutes between moonrise on the 2 successive nights nearest the full moon closest to the vernal equinox. Moonrise data were obtained from the US Naval Observatory webpage (http://aa.usno.navy.mil/AA/data/). Lag indices were created in each of the climatological variables by offsetting the index value by 1 year.

Initial Pearson product-moment correlations were calculated between the monthly climate indices and mean NABBS counts of bobwhite in Illinois; these tests were performed to winnow the array of variables to a smaller suite of variables most likely influential to bobwhite population dynamics. Bobwhite abundance was then related to climate indices in multivariate autoregressions; the autoregressions accounted for the density-dependent nature of bobwhite population dynamics and the correlation of

Table 6.1. Source and world wide web location for oscillation indices.

Index	Source	URL
PDO	Joint Institute for the Study of the Atmosphere and Oceans	ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/INDICES/PDO.latest
ENSO	Joint Institute for the Study of the Atmosphere and Oceans	ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/INDICES/nino34.long.latest
AO	Department of Atmospheric Science, Colorado State	http://www.atmos.colostate.edu/ao/Data/ao_index.html
NAO	Climate and Global Dynamics Division of the National Center for Atmospheric Research	http://www.cgd.ucar.edu:80/cas/climind

abundance between any 2 consecutive years (Chapter 4). When analysis of multicollinearity indicated a pair of climate variables were highly related, the 1 of the pair explaining less variation in bobwhite abundance was dropped. An all-possible models analysis was then conducted for the remaining variables, examining each potential combination of climate variables. The models minimizing Aikike's Information Criterion were selected as candidate models (Burnham and Anderson 1998). Autocorrelation of residuals, the Portmanteau statistic, and the Box-Ljeung statistic were plotted as tests of the goodness-of-model fit. Aikike weights were calculated for each model to gain insight into the relative strength of each model in projecting Truth. Model averaging was conducted based on these Aikike weights (Burnham and Anderson 1998).

RESULTS

Temporal Patterns

State-wide Climate.-Spring temperature (SPRTEMP) was consistently positively related to annual bobwhite abundance (all ρ's > 0.122, $\bar{x}$ = 0.279), whereas both of the winter parameters, total number of days of snow >2.54 cm (SNWDYS) and total winter snow (TSNW), were negatively related (Fig. 6.2). In all years, SNWDYS was negative (all ρ's < -0.059, $\bar{x}$ = -0.228), whereas in 1 year, 1969, TSNW was positively related to bobwhite abundance. In all other years, though, TSNW also was negatively correlated to bobwhite abundance (except for 1969, all ρ's < -0.045, $\bar{x}$ = -0.216). The coefficient of variation in spring temperature (CVTEMP) also was negatively related to bobwhite abundance (all ρ's < -0.082, $\bar{x}$ = -0.270). Neither the coefficient of variation in spring

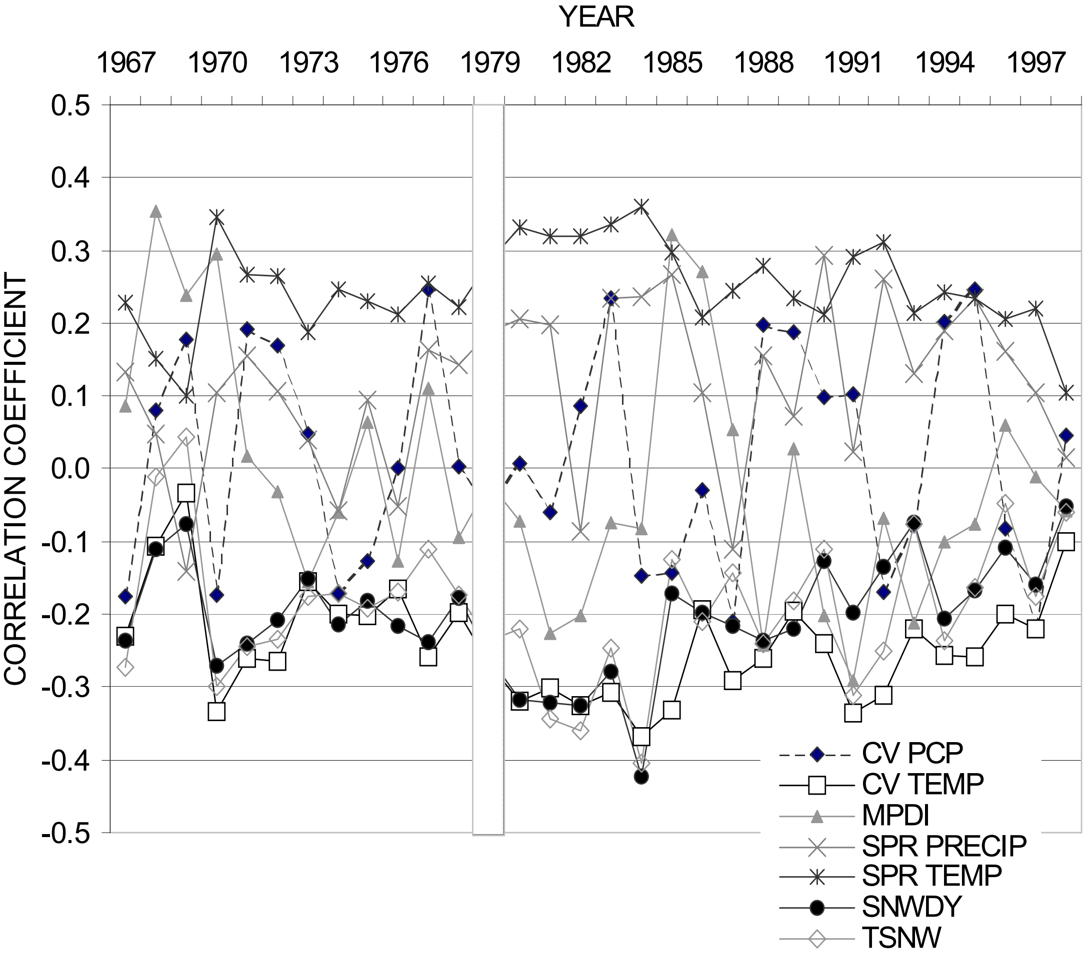


Figure 6.2. Pearson product-moment correlations between mean Northern Bobwhite count as determined by the North American Breeding Bird Survey and weather parameters. Acronyms are provided in text. Indices of bobwhite abundance indicated a sharp decline in abundance in 1979, which is highlighted in this figure.

precipitation (CVPCP; $\bar{x} = 0.011$) nor the Modified Palmer Drought Severity Index (MPDSI; $\bar{x} = -0.019$) were related to bobwhite abundance.

Based on standardized NABBS counts for the state, multivariate autoregression indicated bobwhite abundance was a function of abundance in past years, number of days with snow >2.54 cm, and annual drought severity. The model was:

$$X_t = 0.810X_{t-1} - 0.395X_{t-3} + 0.374X_{t-4} - 0.013(\mathrm{SNWDY}) + 0.007(\mathrm{MPDSI})$$

(AIC = 17.55, $R^2 = 0.85$).

Global Climate Analyses.–Correlations and examination for multicollinearity reduced the number of potentially explanatory variables to 42. These included 3 indices of PDO (including 1 lagged variable), 17 for ENSO (7 lagged variables), 10 for AO (7 lagged variables), 11 for NAO (5 lagged variables), and Lunar Nodality.

Pearson product-moment correlations relating individual climate indices to mean bobwhite counts indicated the Pacific Decadal Oscillation (PDO) for May was the most highly correlated climate parameter (Fig. 6.3). However, this ignored temporal autocorrelation in the bobwhite time series, resulting in an inflated observed correlation. After considering PDO (May) and the other variables in a multivariate setting accounting for temporal autocorrelation, PDO (May) was no longer the most explanatory variable (Table 6.2).

Two models were particularly informative, a 6- and a 7-variable model (AICc = 139.1 and 140.6, $R^2 = 0.73$ and 0.77, respectively). Aikike weights ($w_{\text{6-variable}} = 0.677$ vs. $w_{\text{7-variable}} = 0.323$) suggested the former model was twice as informative in explaining variation in the loess detrended time series of bobwhite abundance (Fig. 6.4). The final

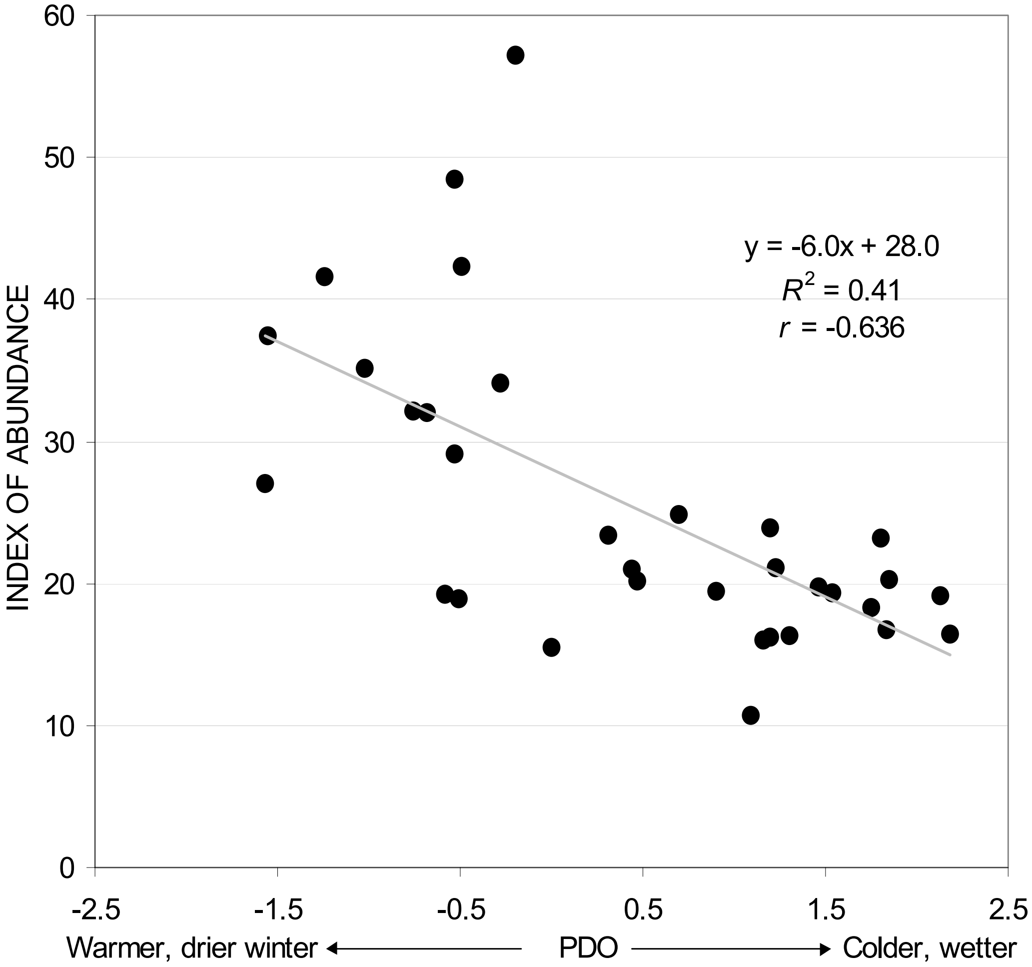


Figure 6.3. Least-squares regression of mean annual North American Breeding Bird Survey counts of Northern Bobwhite and the Pacific Decadal Oscillation (PDO), as

annually measured in May.

Table 6.2. Parameter coefficients for the top 10 multivariate autoregressions relating global climatological phenomena to detrended mean annual North American Breeding Bird Survey counts of Northern Bobwhite; models are listed from most to least explanatory. AR is the autoregressive parameter coefficient. ΔAIC is the difference in AIC units between the best model (i.e., the model with the lowest AIC) and the nominate model. AIC weights are the relative model confidence.

AIC_c	K	AR(1)	AR(2)	AR(3)	AR(4)	ENSO	AO	PDO	ENSO	ENSO	ΔAIC	w_i (<	w_i (≤2
139.083	6	0.304	-0.065	-0.580	-0.106	1.325		-0.257			0.000	0.257	0.677
140.564	7	0.175	-0.182	-0.459	-0.245		1.184	0.104	-0.658		1.481	0.123	0.323
141.826	7	0.228	-0.176	-0.462	-0.202		1.107	0.109		-0.615	2.743	0.065	
142.025	6	0.236	-0.154	-0.468	-0.176			-0.002	-0.704		2.942	0.059	
142.224	7	0.269	-0.095	-0.537	-0.158	1.073		-0.190	-0.411		3.141	0.053	
142.380	6	0.267	-0.152	-0.469	-0.152			0.016		-0.716	3.297	0.049	
142.578	7	0.290	-0.092	-0.541	-0.138	1.075		-0.177		-0.400	3.495	0.045	
142.632	5	0.282	-0.194	-0.445	-0.153					-0.872	3.549	0.044	
142.701	6*	0.279	-0.149	-0.474	-0.136			0.038			3.618	0.042	
142.797	7*	0.241	-0.172	-0.467	-0.184		1.068	0.120			3.714	0.040	

* Additional explanatory variable was ENSO, September (Lagged 1), with coefficients = -0.794 and -0.644, respectively.

models were written as:

Model A $X_t = 0.304X_{t-1} - 0.065X_{t-2} - 0.580X_{t-3} - 0.106X_{t-4} + 1.325(\text{ENSO}_{\text{Aug}}) - 0.257$
$(\text{PDO}_{\text{July Lagged 1}})$.

Model B $X_t = 0.175X_{t-1} - 0.182X_{t-2} - 0.459X_{t-3} - 0.245X_{t-4} + 1.184(\text{AO}_{\text{Apr}}) + 0.104$
$(\text{PDO}_{\text{July Lagged 1}}) - 0.658(\text{ENSO}_{\text{Nov}})$.

The mean effect of the PDO delayed 1 year was negative, and was context dependent in that when ENSO for August was included in the model, PDO was negative, but when ENSO for November was included, PDO was positive.

Burnham and Anderson (1998) provided a means by which an average model, combining the 2 models based on Aikike weights (*w*), could be calculated. The average model was:

$$X_t = 0.262X_{t-1} - 0.103X_{t-2} - 0.541X_{t-3} - 0.151X_{t-4} - 0.140(\text{PDO}_{\text{July Lagged 1}}) + 0.897(\text{ENSO}_{\text{Aug}}) - 0.212(\text{ENSO}_{\text{Nov}}) + 0.382(\text{AO}_{\text{Apr}}).$$

This averaged model demonstrated a positive relationship between abundance in any 2 years, but negative abundance between the current year and the 3 years prior to the previous year. Climate elements in fall decreased abundance, whereas elements in spring were associated with increased quail abundance. Climate elements in summer were contradictory, promoting abundance in some instances and decreasing abundance in other instances, depending on the phase and strength of each process. Perhaps surprisingly, no explicit winter variables were included in the models.

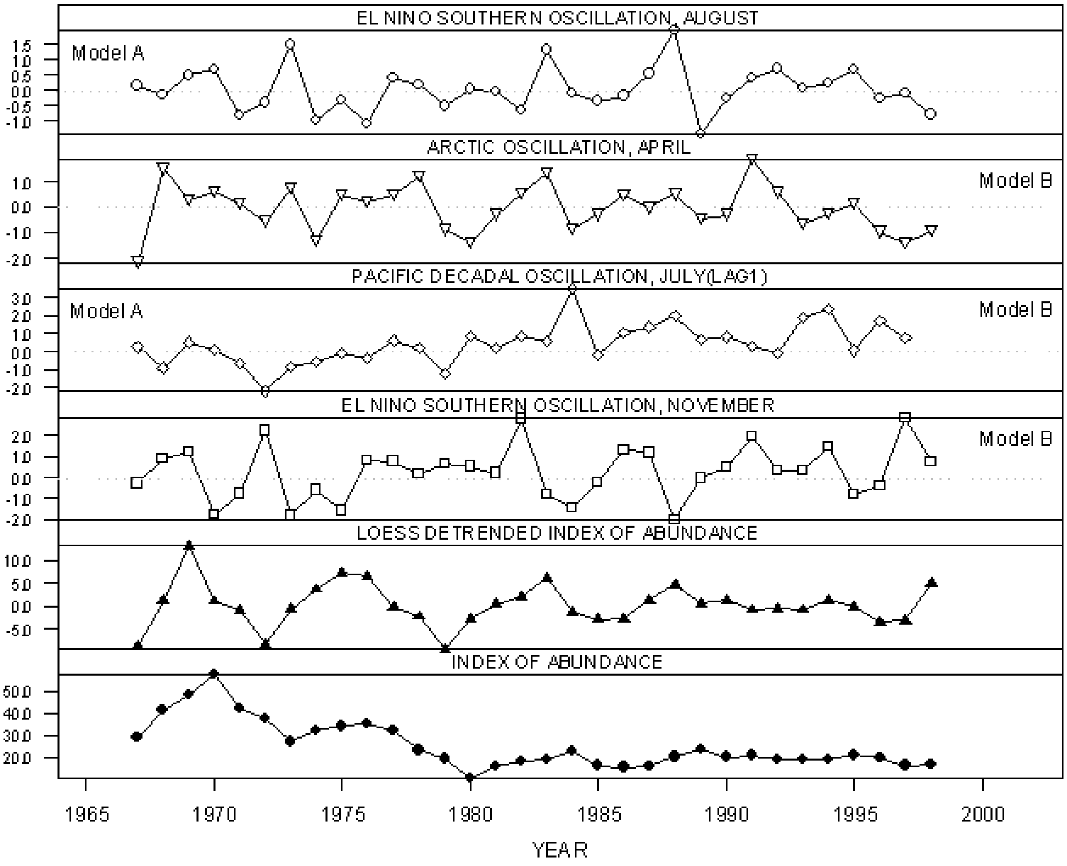


Figure 6.4. Time series plots of bobwhite abundance indices and explanatory variables. Model A refers to the first (6 variable) model in Table 6.2, whereas Model B refers to the second (7 variable) model.

Spatial Models

State-wide Climate.–Given the temporally consistent influence of the significant variables, I examined spatial influence. I used general linear models rather than a spatial linear modeling framework because I was more concerned with explaining large-scale trends in bobwhite abundance.

Bobwhite abundance varied spatially as a function of weather (Table 6.3). In general, though, climate predicted little of the spatial variation in annual abundance; most model R^2s were <0.25, and the mean model R^2 was <0.07. Similar results were observed when analyses were restricted to predicting annual presence/absence with logistic regression. Encouragingly, parameter estimates were in the expected direction. For instance, snow coverage (TSNW and SNWDY) and the variation in spring temperature (CVTEMP) consistently exhibited a negative effect on abundance, whereas spring temperature and precipitation (SPRTMP and SPRPCP) positively contributed to abundance. Variation in precipitation in spring (CVPCP) and through the year (MPDSI) had little consistent (i.e., mean) effect even though their effect annually was often significant.

Multivariate models generally indicated some combination of spring precipitation, drought severity, number of days with snow >2.5 cm, and variation in spring precipitation contributed to spatial variation in annual abundance (Table 6.4). Model R^2s were again generally low for all models, in this case indicating that when climate was relatively consistent state-wide the effect of climate on abundance was less evident spatially.

Mean bobwhite abundance for 1985–1998 was related in a complex model of

Table 6.3. Mean parameters from univariate general linear models regressing bobwhite abundance against spatially-explicit climatological predictors. Years refers to the number of years (1967–1998, *n* = 32) in which regression was significant.

Parameter	Years	Intercept (SE)	β_1(SE)	R^2 (range)
TSNW	28	1.059 (0.208)	-0.423 (0.051)	0.035 (0.001-0.0149)
SNWDY	30	0.970 (0.317)	-0.452 (0.081)	0.046 (0-0.209)
SPRTEMP	31	-5.505 (0.451)	1.951 (0.166)	0.057 (0.001-0.224)
SPR PCP	25	-4.528 (0.911)	0.856 (0.193)	0.031 (0-0.195)
CVTEMP	24	-0.785 (0.416)	0.033 (0.099)	0.027 (0-0.124)
CV PCP	31	4.510 (0.417)	-1.258 (0.101)	0.058 (0.001-0.239)
MPDSI	27	-0.578 (0.119)	0.069 (0.006)	0.069 (0-0.315)

EASTING and NORTHING and their interaction, with the geographical coordinates raised to the 2nd and 3rd powers ($F_{7,2287} = 222.0$, $P < 0.0001$, $R^2 = 0.405$). I attempted to account for this large-scale geographical variation by applying mean climatological conditions to bobwhite abundance, realizing that some large-scale variation in abundance due to weather would be left unaccounted for because climate has a cumulative rather than mean effect. A 3-variable model was chosen ($F_{3,2291} = 268.2$, $P < 0.0001$, $R^2 = 0.260$).

The residuals from the 3-variable model exhibited slight non-normality in a normal quantile plot, as expected given the remaining small-scale autocorrelation in abundance. Remaining large-scale variation after application of the model occurred along a northeast-southwest gradient whereas trend in the northerly direction was absent. This indicated effects of winter climate on bobwhite abundance were accounted for whereas larger trends due to landform heterogeneity remained. To discern whether additional residual variance may be explained in this large-scale trend, elevation and row crop (Illinois Department of Natural Resources 1996) abundance at multiple spatial scales were assessed along with the climatological variables. Elevation was dismissed because it was highly collinear with SPRPRCP and TSNW; row crop was chosen because I surmised the trend might be due strictly to the abrupt transition from intermixed farm-forest lands in the south and west to the flat agricultural plains of north-eastern Illinois (Table 6.5; Fig. 6.5; $F_{4,2290} = 222.9$, $P < 0.0001$, $R^2 = 0.280$).

Even though the larger model explained only an additional 2% of variation in the large-scale trend, it significantly reduced the unexplained geographic variation.

Inclusion

Table 6.4. Multiple linear regressions of spatially-referenced annual Northern Bobwhite abundance and climatological variables in Illinois.

Year	Intercept	TSNW	SPR PCP	MPDSI	CV PCP	R^2
1967	-1.243	-0.261	0.704	-0.302		0.075
1968	0.854		-0.214	0.040		0.136
1969	3.174	-0.112		0.037	-0.602	0.102
1970	-14.629	0.426	2.422	0.107	-0.210	0.237
1971	-6.646	-0.403	1.921	0.011		0.126
1972	0.891	-0.470		-0.028		0.053
1973	5.707	-0.199	-0.995	-0.021		0.058
1974	-1.280	-0.353	0.563	-0.006		0.019
1975	3.015	-0.531	0.463	-0.024	-0.771	0.062
1976	3.669	-0.399	-0.526	-0.024		0.030
1977	-0.649	-0.403	-0.550	0.020	1.080	0.079
1978	-2.491	-0.400	0.805	-0.022		0.019
1979	-9.251		2.089	-0.014	-0.531	0.061
1980	-11.552	-0.494	2.843	-0.008		0.075
1981	-8.200		0.792	-0.032	0.726	0.099
1982	-10.206	-0.248	2.092	-0.027	0.473	0.083
1983	-2.205	-0.328	0.610	-0.007		0.043

Table 6.4. Continued.

Year	Intercept	TSNW	SPR PCP	MPDSI	CV PCP	R^2
1984	-11.753	-0.557	2.830	-0.046		0.081
1985	-4.650		0.927	0.074	-0.420	0.194
1986	0.500		-0.414	0.085	-0.207	0.125
1987	5.578		-0.904	0.021	-0.746	0.045
1988	0.005	-0.292		-0.035		0.104
1989	-1.672		-0.597	0.005	0.931	0.036
1990	-6.399		1.150	-0.028		0.073
1991	2.439		-0.766	-0.054	0.373	0.130
1992	-2.695	-0.365	0.322	0.422		0.024
1993	0.277			-0.029	-0.174	0.056
1994	-3.747		-0.325	-0.024	1.229	0.037
1995	-10.391	-0.131	1.103	-0.040	1.075	0.063
1996	-2.505	-0.508	0.707	0.043		0.031
1997	-2.225		0.464	0.004	-0.218	0.012
1998	0.990	-0.072				0.017

Table 6.5. Model accounting for large-scale trend in Northern Bobwhite abundance in

Illinois, between 1985 and 1998.

Parameter	β	SE	*t*	*P*
Intercept	-0.5074	0.0369	-13.77	<0.0001
SPRPRCP	0.0356	0.0015	22.96	<0.0001
MPDSI	-0.0050	0.0009	-5.57	<0.0001
CVPRCP	0.0057	0.0005	12.10	<0.0001
Row Crop$_{5,000\ \text{ha}}$	<0.0001	<0.0001	-8.04	<0.0001

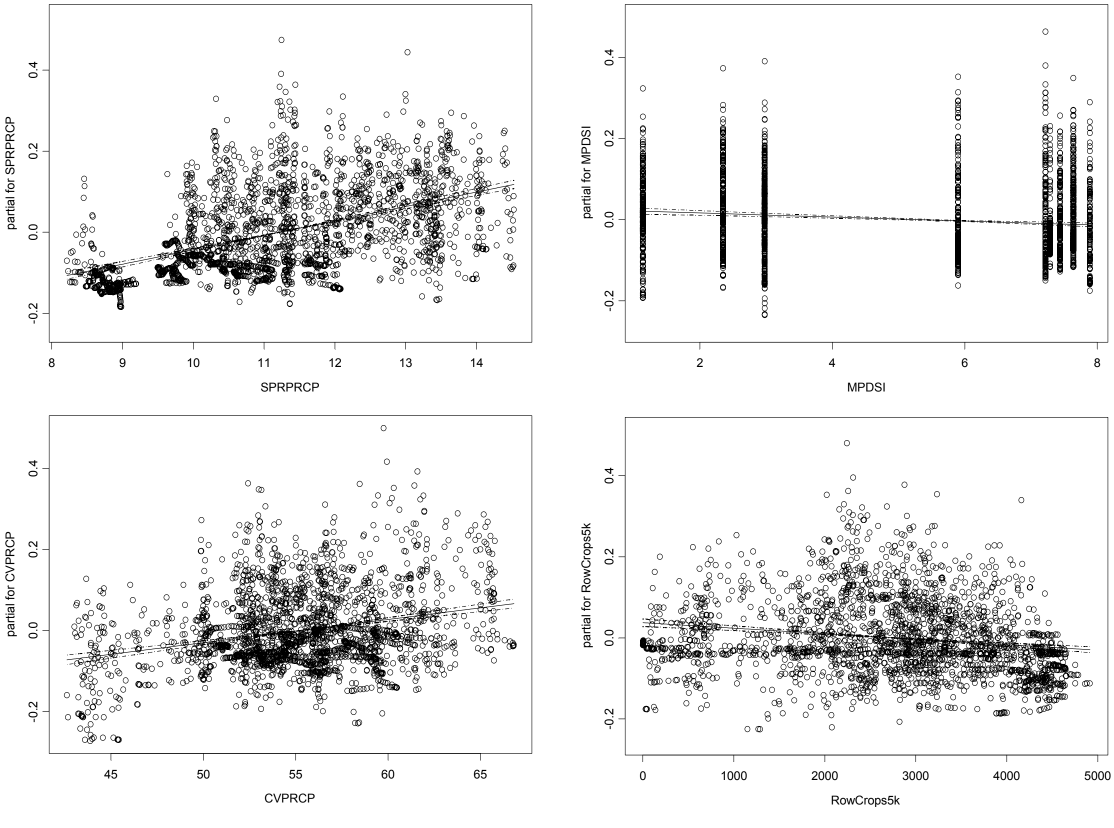


Figure 6.5. Partial regression plots demonstrating relative influence of climatological (SPRPRCP, mean spring precipitation (cm); MPDSI, modified Palmer Drought Severity Index; CVPRCP, coefficient of variation in mean spring precipitation) and land use (amount (ha) of row crop agriculture in 5,000 ha landscape) conditions on regional trends in Northern Bobwhite abundance in Illinois, 1985–1998.

of EASTING and NORTHING in the model did not improve model fit due to collinearity with CVPRCP and SPRPRCP, respectively. Thus, residuals from this final model were used in models examining association between bobwhite abundance and landscape environmental characteristics (Chapter 7).

DISCUSSION

Historical climatological factors can have persistent effects on animal abundance by reducing breeding productivity and annual survival, thus lowering annual abundance. Since population dynamics are multiplicative, these effects in any 1 year can ripple across subsequent years. Relationships between proximate weather conditions and quail ecology are well-demonstrated (see Introduction). In this chapter I have shown relationships exist at higher scales between quail abundance and both regional and global climate indices. These relationships are not simple.

Previously, above average amounts of precipitation when temperatures are cool during the breeding season have been shown to result in greater breeding activity (Robinson and Baker 1955, Speake and Haugen 1960, Guthery et al. 1988), and my results concur. At a regional scale, spatial models indicated spring precipitation, annual drought severity, and winter snowfall influenced annual quail abundance. Areas where snowfall the previous winter was high were generally associated with lower spring abundance, whereas areas where spring precipitation was high were generally positively associated. In southern Illinois, Roseberry and Klimstra (1984) found quail abundance was positively related to total precipitation between 22 March and 30 April and negatively related to snow cover ≥2.5 cm.

While model performance was low for all spatial models, the similarity of effect across years suggests that the effect of these parameters is real. Univariate measures suggested little effect of annual drought severity on Illinois quail abundance. This is contrary to the findings of Bridges et al. (2000), where, in Texas, bobwhite were highly associated with annual MPDSI ($r = 0.91$). The effect of MPDSI in Illinois was only seen when in combination with other regional climate variables after the effects of serial abundance were accomodated, and generally acted to offset the positive effects of spring rain and complement the negative effects of winter precipitation.

Global climate processes may significantly influence life-history characteristics of terrestrial species (Forchhammer et al. 1998*a*,*b*; Post et al. 1999). I have shown, for the first time, the effect of global climate on quail. The final model relating large-scale weather phenomena to quail abundance in Illinois indicated when the Pacific Decadal Oscillation was high (*warm* phase), such as in 1992, 1993, and 1997, abundance was depressed the following year (e.g., 1993, 1994, and 1998). Warm phase PDO in the summer yields increased precipitation, but its effect on bobwhite was not seen until the following year. Why summer precipitation in the previous year should influence quail abundance is unclear. It may be that the relationship is spurious. However, of the variables considered, PDO lagged 1 year showed a consistently strong effect across the models studied. It was, however, negatively related when included in models with $\mathrm{ENSO}_{\mathrm{August}}$ and positively related in models with $\mathrm{AO}_{\mathrm{April}}$ and $\mathrm{ENSO}_{\mathrm{November}}$. The effect of the lag may be explained in that increased precipitation in the previous summer may foster a response in vegetation, leading to an increased rate of succession or tillage, disrupting quail population dynamics. In Chapter 4 I noted the occasional occurrence of delays in density-dependence; PDO lagged 1 year is a promising source for this lag in density dependence. Clearly, until further data are available, this connection with PDO should be interpreted cautiously.

When the Arctic Oscillation in April was negative, blasts of cold air shot into the Midwest, resulting in the delay of spring green-up and subsequent breeding phenology. The El Niño Southern Oscillation had a more complex effect on abundance, encouraging higher abundance in August and depressing abundance in November. During warm phases (El Niño), late fall and early winter temperatures were milder than usual, whereas during cold phases (La Niña) the probability of and amount of precipitation increased. The warmer temperatures associated with El Niño typically resulted in 25–50 cm less snowfall in northern Illinois and 2.5–25 cm less snowfall in southern Illinois (Mantua et al. 1997). Connections between ENSO and Midwest climate are strongly dependent on the phase of the PDO, such that the “typical” or “canonical” patterns of ENSO are only valid when ENSO and PDO are in phase (Nigam et al. 1999). That both PDO and ENSO were included in the final model of abundance further demonstrated the connection between these 2 climate processes.

CHAPTER SEVEN

FACTORS INFLUENCING EXTANT DISTRIBUTION AND ABUNDANCE: ACCOUNTING FOR SPATIAL AUTOCORRELATION AND HISTORICAL EFFECTS

All models are wrong, some are useful,
and we should seek out those.
George Box, statistician

Eventually you stop trying to visualize [higher extra dimensions].
That's when the roar goes out of your ears.
Adam Frank, astrophysicist

Identifying factors limiting abundance and distribution of wildlife is essential to understanding their population dynamics. Unfortunately, this is difficult because of problems in assessing the relative importance of various factors acting in concert such as weather, inter- and intra-specific interaction, and habitat. In Chapter 3 I examined intra-specific interaction *vis a vis* density dependence and in Chapter 6 I examined effects of weather. In this chapter, I examine the influence of habitat on bobwhite abundance and distribution through the implementation of a spatially-explicit wildlife-habitat model.

Spatially-explicit wildlife-habitat models formalize our understanding of the relationship between wildlife species and the environment, leading to a greater understanding of which environmental factors affect wildlife distribution and abundance (Morrison et al. 1998). Once these environmental factors have been identified, and their relative contribution to population and community dynamics are known, predictions may be made regarding wildlife distribution and abundance. For birds, the typical means of assessing a response by a species to an environmental factor is through the use of point counts.

Robbins and Van Velzen (1967:2) stated point counts, NABBS locations in particular, do “not pretend to measure the number of birds present in an area,”, but rather, provide “an index of abundance that can be used for detecting changes from year to year.” However, a positive relationship between the number counted and the number actually in an area is assumed (Linehan 1968). Therefore, it follows that a relationship between this number and habitat in an area locally about the survey station must occur as well, especially if density and habitat quality are positively related.

Point counts at individual road-side stations (stops) have rarely been examined in relation to local habitat. Emlen and Wiens (1965, Wiens and Emlen 1966) related relative coverage of general vegetation types at road-side point counts to the distribution and abundance of Dickcissel (*Spiza americana*) in Wisconsin. Baker (1977) related habitat to the abundance of 115 bird species at NABBS points in northern California. Wiens and Rotenberry (1981:524), noted limitations in the accuracy of road-side point counts made “detailed and precise habitat measurements” impractical, but suggested patterns of general habitat affinities are discernible from remotely-sensed data.

Numerous statistical models have been developed for predicting suitability of habitat for wildlife over large areas based on limited counts. These methods include, but are not limited to, linear regression (Morrison et al. 1987, Ward et al. 1991, Rice et al. 1993, Puttock et al. 1996, Li et al. 1998, Penhollow and Stauffer 2000) and logistic regression (Nadeau et al. 1995, Pausas et al. 1995, St. Georges et al. 1995, Pearce and

Ferrier 2000, Penhollow and Stauffer 2000). These models, however, typically fail to account for one of the assumptions of linear modeling.

The traditional independence assumption in linear and logistic regression holds that the error terms corresponding to different survey points are not correlated in time or space (Neter et al. 1989). When the error terms are serially correlated (autocorrelated), ordinary least squares produces biased estimates of the standard errors of the regression coefficients (Choudhury et al. 1999). These biased standard errors lead to confidence intervals which are too narrow, increasing the likelihood of spurious relationships (Legendre 1993). Numerous authors have found that disregarding the effects of autocorrelation leads to over-estimation of the importance of habitat variables due to a bias in the slope parameter (Robertson 1987; Anselin 1989; Klute et al. 2001). Ignoring autocorrelation also may lead to inclusion of unimportant model covariates (Legendre 1993, Wu and Huffer 1997).

A few ecologists are beginning to account for spatial dependencies in their data when modeling the distribution or presence/absence of a species. Researchers accounting for spatial autocorrelation have sometimes removed the spatial structure prior to model building, whereas others have exploited the underlying spatial autocorrelation with geostatistics to improve fit of predictive models (Le Duc et al. 1992, Liebhold et al. 1993). The former strategy generally produces a general model translatable to portions of the species range outside of the immediate area of interest, whereas the latter strategy generally produces more accurate predictions of species occurrence.

Examples of the latter strategy are becoming common. Autologistic regression has previously been used to model presence of American woodcock (*Scolopax minor*) in Pennsylvania (Klute et al. 2001) and plant species distribution in Florida (Wu and Huffer 1997). Beard et al. (1999) took a similar approach to modeling breeding bird distribution in Idaho. Augustin et al. (1996) incorporated autocorrelation effects in logistic regression models of deer distribution in England. This approach explicitly accounts for spatial autocorrelation by modeling the log odds of the categorical response as a linear combination of both ecological covariates and responses at neighboring sites (Cressie 1993). A large amount of information is lost, however, when analyzing presence/absence in logistic regression analyses when abundance data are available. Few ecological studies, however, have accounted for correlated errors in linear models of species abundance; Stralberg and Bao (1999) are a notable exception. In this chapter, I account for correlated errors in a hierarchical fashion, modeling first bobwhite presence and then abundance, with models of abundance accounting for spatial autocorrelation in the errors.

In Chapter 5, I interpolated bobwhite abundance based on the assessed autocorrelation structure from >2,600 survey sites located across Illinois. These interpolations of abundance, however, did not account for local-area and landscape-level habitat, which may potentially exert greater influence over abundance than would neighborhood effects alone. In this chapter, I assessed the influence of environmental parameters within a spatial linear modeling framework. Given a linear regression model $y = \mathrm{X}\beta + e$, small-scale spatial autocorrelation was incorporated by fitting an autoregressive covariance model to the errors. The spatial and regression parameter estimates interacted, and the model was fitted iteratively (MathSoft 2000).

METHODS

Data

The models were parameterized with NABBS call count data for 1985–1998, the period when satellite imagery was taken (1989–1992) of the Illinois landscape. The model of bobwhite abundance may be improved if call count numbers were related to the time of day counts were conducted. Wilson (2000) found bobwhite calling peaked between 45 and 50 min after sunrise in Oklahoma, and counts differed by as much as 3 times depending on when the count occurred. Effect of time when NABBS counts were conducted on the number of bobwhites counted was ameliorated by using only the 30 intermediate stops on every route and by averaging across 14 years of counts; Elder (1956) also eliminated counts (those 30 min before sunrise) because of large variability in number observed.

Habitat Variables

Bobwhite habitat was assessed at multiple spatial scales (Wiens et al. 1987). Land use/land cover (Illinois Department of Natural Resources 1996), elevation, slope, aspect, soil type, and distance to watercourse were examined at each NABBS survey site (~0.08 ha). Digital data files of elevation and soil are available from the Illinois Geospatial Data Clearinghouse (http://www.isgs.uiuc.edu/nsdihome/webdocs/browse.html). These variables and others also were calculated for 5-, 50-, 500-, and 5,000-ha buffers around the survey location (Table 7.1). Configuration metrics for land use/land cover class and landscape were calculated with the grid version of PATCH ANALYST (Grid 2.1; Carr et al. 2000), an ArcView extension implementing FRAGSTATS (McGarigal and Marks 1995) in a menu-driven manner (Appendix 7.A); the particular script used for these calculations was originally written by Gary Mohr (Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale).

Determining Distribution

I assessed the influence of environmental parameters on bobwhite distribution with logistic regression. Given that ecological theory generally prescribes a sigmoid curve for species tolerance over part of an occupied gradient, it is reasonable to operate on the assumption that species occurrence relates to an environmental gradient in a logistic rather than linear manner (Osborne and Tigar 1992).

Logistic regression models are generalized linear models where:

ln(Probability of Event/Probability of No Event) = ln(*odds*) = $\alpha + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_n x_n$, where ln is the natural log. For any logistic regression, the odds of an event (or no event) given a set of conditions can be determined by calculating:

$$odds = e^{\alpha + \beta 1x1 + \beta 2x2 + ... + \beta nxn}.$$

Probability of an event occurring is calculated as:

Habitat Suitability Index (HSI) = Probability of Occupation = *odds*/(1 + *odds*).

To account for the influence of severe winters of the late 1970s on current distribution, I considered weather parameters from 1977–1979 (Chapter 6).

Model goodness-of-fit was assessed in 2 ways, with the Brier score (Brier 1950, Epstein 1988, Murphy 1993, Margolis et al. 1998) and the leCessie-vanHouwelingen-Copas-Hosmer (C-H-C-H) goodness of fit test (Hosmer et al. 1997). The Brier score is the mean of the mean squared error between the predicted and observed events. Scores vary between 0 and 1, with a more accurate model closer to 0. A model agreeing with the known outcome 50% of the time has a score of 0.25. The C-H-C-H goodness of fit test is an improvement on the Hosmer and Lemeshow goodness-of-fit test. Classification accuracy was assessed with 3 independent data sets, IDNR bobwhite call count sites for 1990, CBC, and IDNR pheasant call counts. Only presence was validated with CBC and IDNR pheasant call counts and not areas where bobwhite were predicted to be absent.

Determining Abundance

If habitat measures are biologically meaningful to bobwhite, then relative bobwhite abundance should vary across sites as the sites vary in their habitat. I tested this hypothesis with spatial linear models, accounting for the anticipated correlation between counts at adjacent survey sites (Chapter 5). Mean abundance ($\log_{10}$-transformed $\text{mean}_{1985\text{-}1998}$) calculated for the 14-year period around when imagery was taken for the digital land use/land cover of Illinois was used. To remove the north-south trend in bobwhite abundance, I obtained residuals from a model relating historical climatological and land use variables (Chapter 6). These detrended residuals were used in spatial linear models accounting for relative bobwhite abundance with environmental variables and the effects of neighboring survey locations.

A linear model, in its most general form, is comprised of a systematic or predictable component (signal) and an irregular or unpredictable component (noise). A spatial linear model decomposes the predictable component into regional trends (large-scale spatial autocorrelation), local variability (local spatial autocorrelation), and predictor covariates. The spatial linear model (Cressie 1993:406; Eqn. 6.3.9) is written as:

$$\mathrm{Z_i} = \mu_i + \sum_{j=1}^{n} b_{ij}(Z(s_j) - \mu_j) + \delta_i$$

where Z_i is the random process at site i, δ are the errors at site i, and μ_i is the mean at site i described as a linear model with covariates:

$$\mu_i = \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_i x_i.$$

The large-scale trend was accomplished through the preliminary logistic regression delineating occupied habitat.

Determining the proper spatial neighborhood within the occupied habitat is crucial in a properly-performing spatial linear model (Kaluzny et al. 1998). I iteratively fit null spatial models for each neighborhood size between 25 and 65 neighbors. The null model with the lowest residual variance was selected as the appropriate spatial structure in which to evaluate ecological covariates. The spatial and regression parameter estimates interacted and the models were fitted iteratively (MathSoft 2000). Spatial linear models were generated with S-PLUS 2000 (MathSoft 1999), S+SpatialStats (MathSoft 2000), and S-PLUS for ArcView GIS (MathSoft 1998).

Model Selection

Brady et al. (1993, 1998), Schairer (1999), Roseberry and Sudkamp (1998), Michener et al. (2000), and L. W. Burger, Jr. (*personal communication*) examined bobwhite population response to landscape characteristics. I used the variables employed in these studies as a starting point in variable selection (Appendix 7.B). Because it was unclear which suite of variables these authors examined in formulating their final models of presence and abundance, and given little additional theoretical inspiration to guide model selection, I considered >200 variables in building predictive models of bobwhite presence and abundance. An all-possible-models analysis, requiring $2^{>200}$ different models[4], was impractical. To winnow the variables into a manageable suite of candidate variables useful for further modeling, I modeled each variable separately in a univariate spatial linear model. Meents et al. (1983) suggested avian habitat use may be non-linear; I specifically considered non-linear responses by including the square of each variable in my preliminary variable selection procedure.

Aikike's Information Criterion (AIC) was used to rank each variable (Burnham and Anderson 1998), with the most informative variable possessing the minimum AIC. The AIC was corrected for small sample sizes even though n exceeded 1,600 in all analyses. Quasi-likelihood methods were unnecessary since the mean, after removal of the state-wide trend, was normally and continuously distributed, with the mean exceeding the variance. Where terms were different measures of the same effect, and/or highly correlated, I retained the more significant term for further models.

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[4] $2^{>200}$ is equivalent to 1.6×10^{60}, which is greater than the estimated number of stars in the Milky Way galaxy!

An information theoretic approach was followed to determine the most informative suite of multivariate models, with the candidate models ranked by their AIC score (Burnham and Anderson 1998). Candidate models within 2 units AIC were examined in concert (Burnham and Anderson 1998). Where necessary, model averaging was used to define a final model.

Three final models were created. The first model of extant bobwhite distribution accounted for historical effects of weather in a multiple logistic regression with other landscape environmental variables. The second logistic model consisted only of the environmental variables, and demonstrated potentially occupiable land in Illinois. The former model modeled the "true" distribution and bobwhite in Illinois, whereas the second modeled habitat appropriate for bobwhite, regardless of the actual current occurrence of bobwhite. The difference of these 2 maps defined areas of Illinois devoid of bobwhite, but which were suitable for occupancy (Chapter 9). The third model, the spatial linear model, described extant abundance in Illinois.

Mapping Model Results

Two approaches were used to depict model output for maps of habitat suitability. In the Grid module of ArcInfo 8.0 (Environmental Systems Research Institute, Redlands, California) the *focalsum* and *focalmean* commands were used to evaluate, on a pixel-by-pixel basis, the amount of a composition variable within a specified radius of the focal cell (e.g., woodssum = focalsum(woods, circle, 70, data)). Using the original 28.5-m cell initially led to exceedingly long processing times (estimated process times > 1 month);

thus, I resampled the digital Illinois land use/land cover data to 57-m pixels, a pixel 4 times the original cell size (analysis of the resampled land cover took <30 hrs). To evaluate the composition map in conjunction with the configuration maps (described below), the composition map was resampled to the original 28.5-m cell size.

I calculated with PatchAnalyst the identified configuration variable for a set of circular areas (>9,000) placed across the digital coverage of Illinois; these circular areas equaled in size the scale of interest (e.g, 500 or 5,000 ha). The configuration variables identified for the survey locations were then interpolated with ordinary kriging after identification of the underlying spatial autocorrelation by semivariance analysis (Chapter 3 provides details of similar analyses).

RESULTS

Presence/Absence

Composition variables were important in determining presence of bobwhite in the Illinois landscape, whereas configuration variables were important in determining abundance. Whether bobwhite occupied an area was determined by increasing amounts of small grain agriculture and woods, an intermediate degree of evenness of available land classes, and lower elevation. Historical effects of the late-1970s winters on current bobwhite distribution were significant (Appendix 7.C), but in all cases reduced model goodness-of-fit, resulting in their exclusion from the final model.

Because there is a north-south gradient in elevation in Illinois, I assessed the correlation of elevation to mean climate conditions in an effort to discern whether elevation may act as a surrogate for climate. I correlated elevation against mean and departure from mean conditions for each of the regional climate variables examined in Chapter 6 and found mean SNWDY was highly correlated with elevation ($r = 0.84$). Based on this finding, I re-conducted the analyses substituting elevation with mean SNWDY (Table 7.1). Because of the high correlation, differences between the models were negligible, both in model fit and spatial expression.

The model with mean SNWDY rather than elevation described a significant portion of the variance in probability of presence (L.R. $\chi^2_4 = 967.2$, $n = 2{,}460$, $P < 0.0001$) and was well-fitted (Brier = 0.16; C-H-C-H goodness of fit $Z = -0.54$, $P = 0.59$). General model performance was good (Nagelkerke $R^2 = 0.435$, C = 0.837, Tau-a = 0.334). All 3 diagnostics (R^2, C, Tau-a), along with the odds ratios, indicated a model performing considerably better than chance. Margolis et al. (1998) indicated a C > 0.8 provided good predictive ability; a C = 0.837 indicates a randomly selected site will be assigned the correct classification by the logistic regression model 84 times out of 100. Tau-a, a non-parametric correlation statistic, indicated moderate correlation (0.334) between predicted and observed observations, which is about as good as can be expected given the nature of the binary response.

Bobwhite occupied areas with a lower mean elevation (172.8 ± 0.5 m) than was available (188 m; SD = 42.6) and considerably lower than non-habitat (204.6 ± 0.6 m). This elevational difference was likely not the causative agent separating habitat from non-habitat; instead elevation probably masked the influence of the mean number of days of snow >2.5 cm due to a north-south elevational gradient in Illinois. Snow >2.5 cm persisted 10 days less in occupied habitat (28.1 ± 0.3 days) compared to unoccupied habitat (38.2 ± 0.4 days) (Fig. 7.1). Unoccupied habitat experienced 36% more days of

Table 7.1. Influence of environmental parameters on presence/absence of Northern Bobwhite in Illinois, as determined from North American Breeding Bird Survey data. Non-transformed median is provided for occupied (with range) and unoccupied habitat.

Parameter	β	SE	Wald *Z*	*P*	Occupied (Range)	Un-occupied
Intercept	-12.245	1.269	-9.65	<0.0001		
$\log_{10}$(Small Grain$_{5,000\text{ ha}}$)	1.822	0.164	11.12	<0.0001	332 ha (10–1,361 ha)	132 ha
$\log_{10}$(Shannon's Evenness Index)	6.221	2.071	3.00	0.0027	0.62 (0–1)	0.51
$\bar{x}_{\text{SNWDY(1967-1998)}}$	-0.045	0.005	-9.72	<0.0001	27.1 days (12–59 days)	36.6 days
$\log_{10}$(Woods$_{5,000\text{ ha}}$)	0.215	0.126	1.71	<0.0879	906 ha (100–2,817 ha)	746 ha

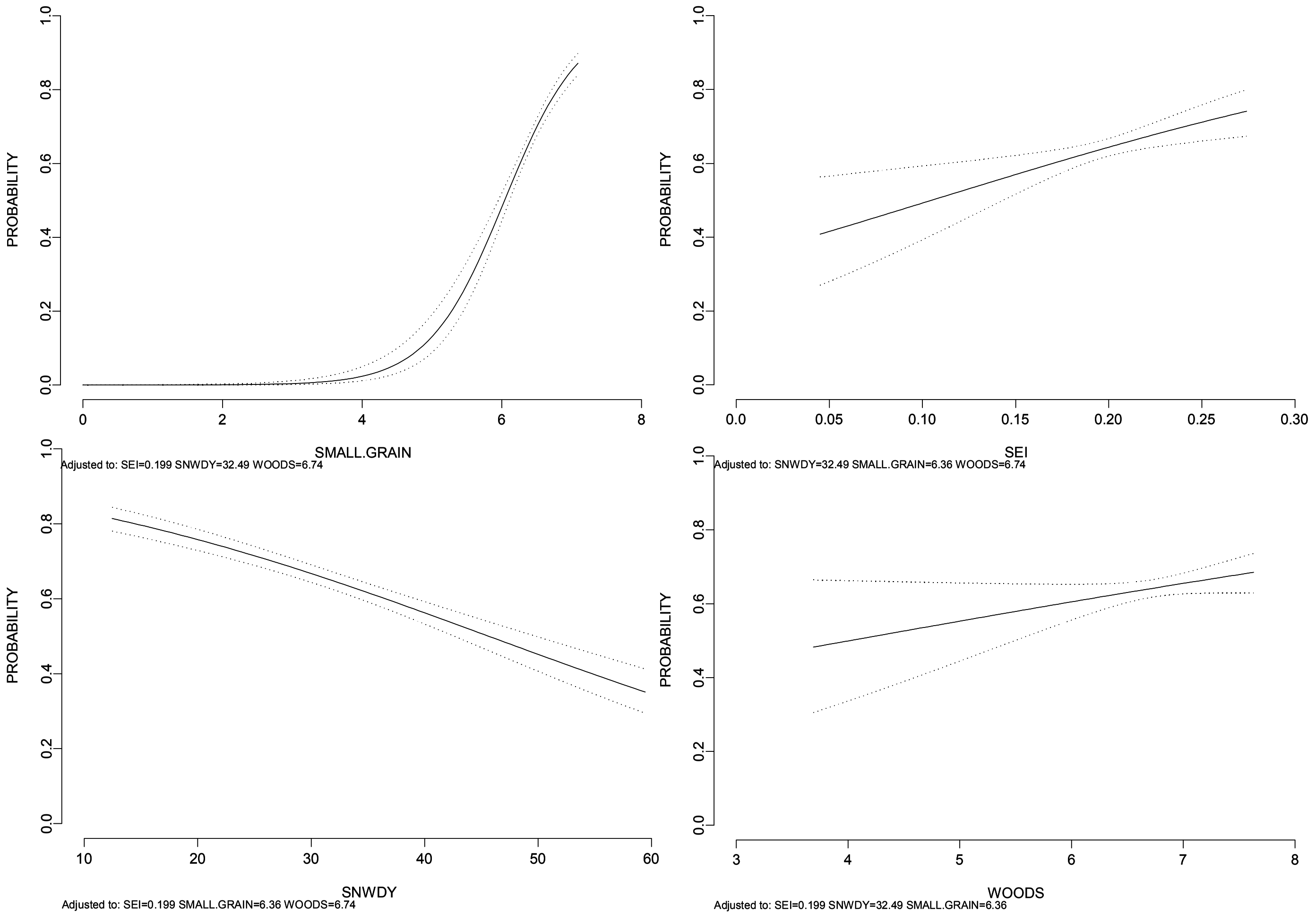

Figure 7.1. Probability plots, with 95% confidence intervals, for each predictor variable in a logistic regression of Northern Bobwhite presence in Illinois, 1985–1998. SEI is Shannon’s Evenness Index, J’.

snow than occupied habitat. Probability of occupancy was <50% for landscapes typically experiencing ≥50 days of snow cover, whereas it was >65% for areas experiencing ≤30 days.

Within a 5,000 ha landscape, there was twice as much small grain agriculture (375.4 ± 3.8 ha vs 172.1 ± 3.0 ha) and 50% more woods (871.7 ± 11.5 ha vs 564.4 ± 11.4 ha) in areas occupied by bobwhites. Probability of occupancy by bobwhite in 5,000 ha landscapes was virtually 0 when small grain agriculture comprised <100 ha; alternatively, landscapes with ≥1,000 ha had ~50% probability of occupancy.

Shannon's J' (Appendix 7.D) was 20% greater in occupied landscapes (0.61 ± <0.01 vs 0.49 ± <0.01). The index approaches 1 as the distribution of different land use classes in the landscape becomes increasingly even, indicating bobwhite occupied landscapes where land use classes were more equitably distributed.

Based on NABBS count data, mean probability of occupation was 0.55 ± 0.01. The mean Habitat Suitability Index (HSI) at unoccupied NABBS sites for the reference year 1990 was 0.457 (LCL = 0.448, UCL = 0.466), whereas the lowest limit for occupied sites was 0.521, a difference of 0.064. There was some overlap of HSI though between occupied and unoccupied sites, as the maximum observed HSI at unoccupied sites was 0.873 and the lowest HSI at an occupied sites was 0.126. Given the apparent break between HSI at occupied and unoccupied NABBS sites, I identified an HSI = 0.50 as the level at which to define patches of suitable bobwhite habitat.

The mean model at HSI = 0.50 predicted 71,294 km^2 (48.9% of the state) of potentially suitable habitat for bobwhite (Fig. 7.2). Because of the curvilinear nature of

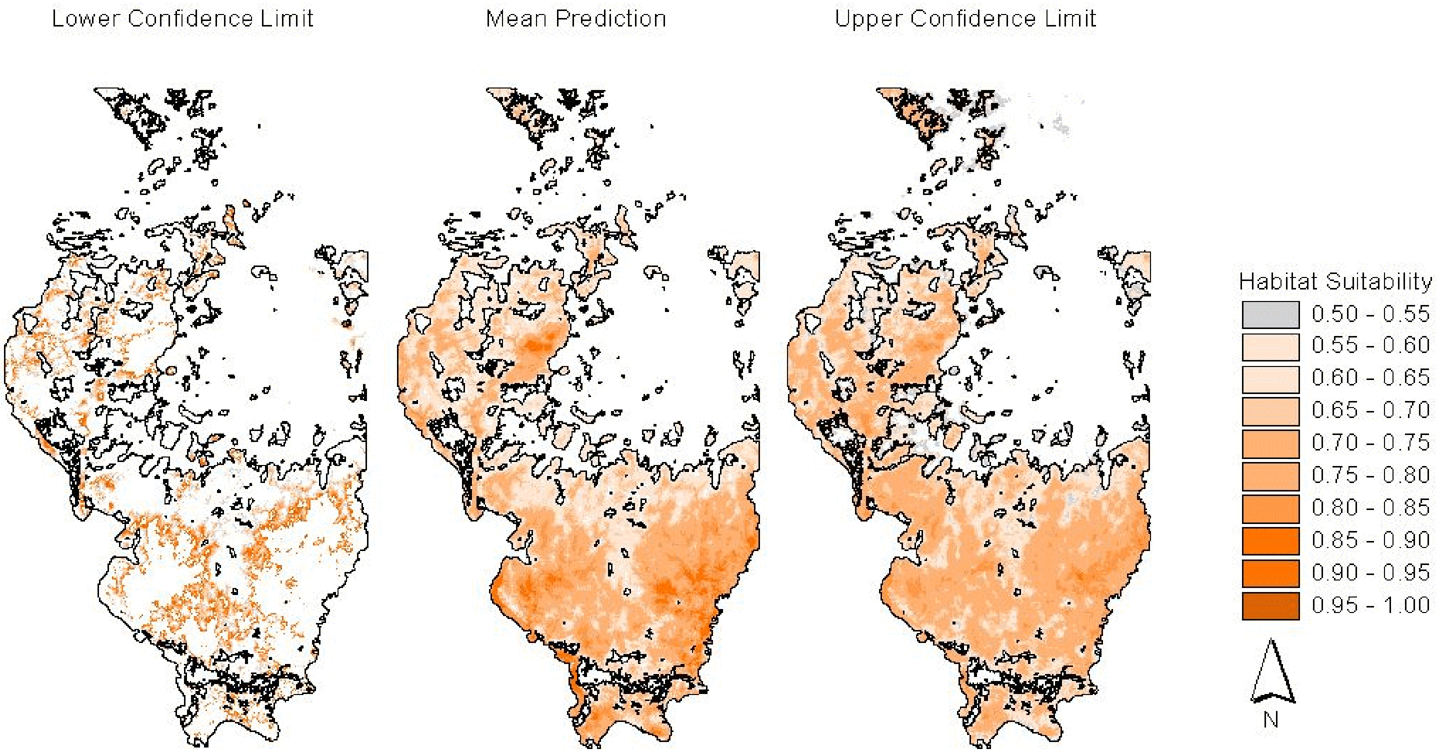

Figure 7.2. Potentially-occupied landscapes for Northern Bobwhite (with lower and upper confidence intervals) in Illinois, as derived from North American Breeding Bird Survey data. The outline delineates mean condition in all 3 plots.

the logistic regression, considerably less habitat was available at the lower confidence level than at the mean or upper confidence levels. The mean and upper confidence levels differed little in total area. The suitability of habitat dropped off quickly, with little habitat at HSI > 0.80 and virtually none at HSI > 0.90 (Fig. 7.3).

Model Validation.–Testing the model of bobwhite presence with IDNR call counts they were predicted to be found. Within the historical quail range, $\bar{x}_{HSI}$ at unoccupied IDNR call count sites was 0.605 ± 0.014 versus 0.666 ± 0.122 at occupied IDNR sites. Because CBC and IDNR pheasant call count routes are most reliable in assessing bobwhite presence rather than their absence, I only compared observations indicating bobwhite presence to the model results. Winter assessments of bobwhite presence (CBC data) indicated a correct-classification rate of 0.783 ($n = 23$); approximate median distance to suitable habitat for those mis-classified CBC locations indicated bobwhite presence was 8.2 km away, generally within the area (12.1-km radius circle) typically surveyed by CBC volunteers. Thus, correct-classification based on CBC data may be as high as 0.913. The IDNR pheasant call counts possessed a correct-classification rate of only 0.335 ($n = 158$).

Abundance

Log-likelihood was maximized for a neighborhood of 62 survey locations (Fig. 7.4; $\log(\mathscr{L}) = -2,650.6$). Based on this neighborhood of 62, abundance was described as a complex

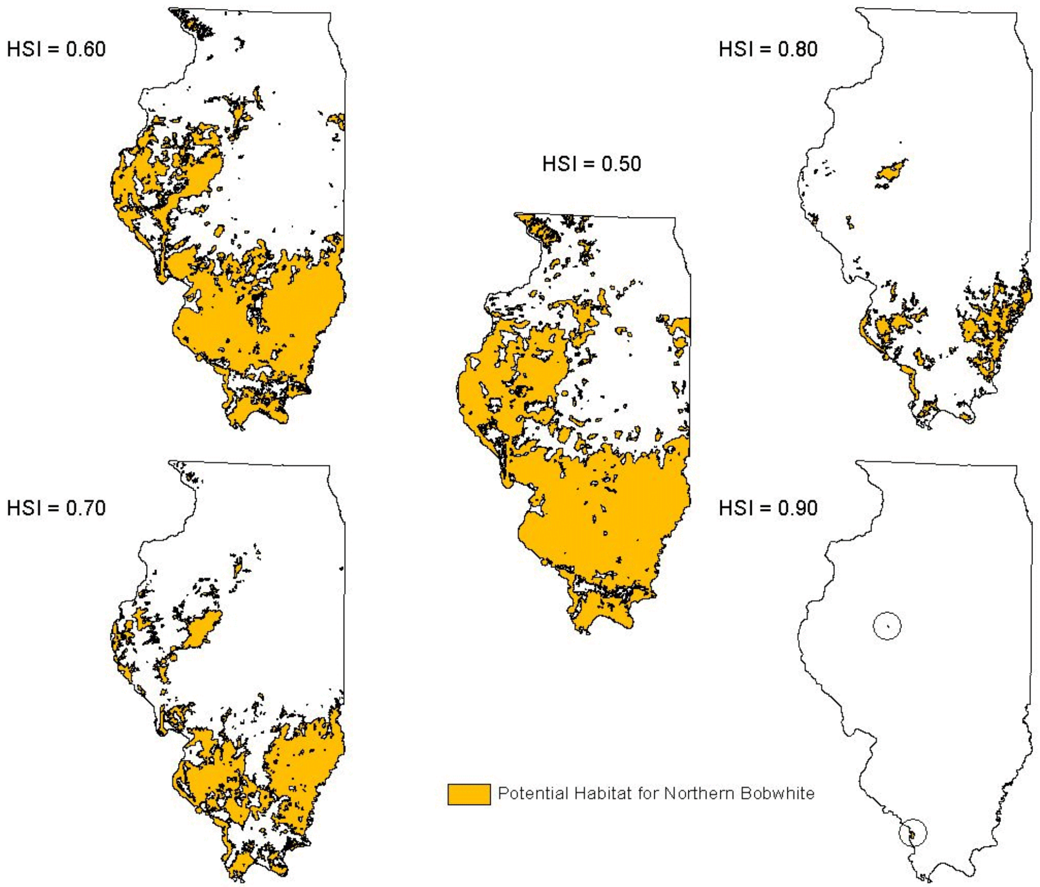

Figure 7.3. Amount of potentially suitable Northern Bobwhite habitat in Illinois at various levels of the habitat suitability index, based on the mean model condition. HSI = 0.50 is the mean condition defining lower limit of suitable habitat. Circles highlight habitat at HSI = 0.90.

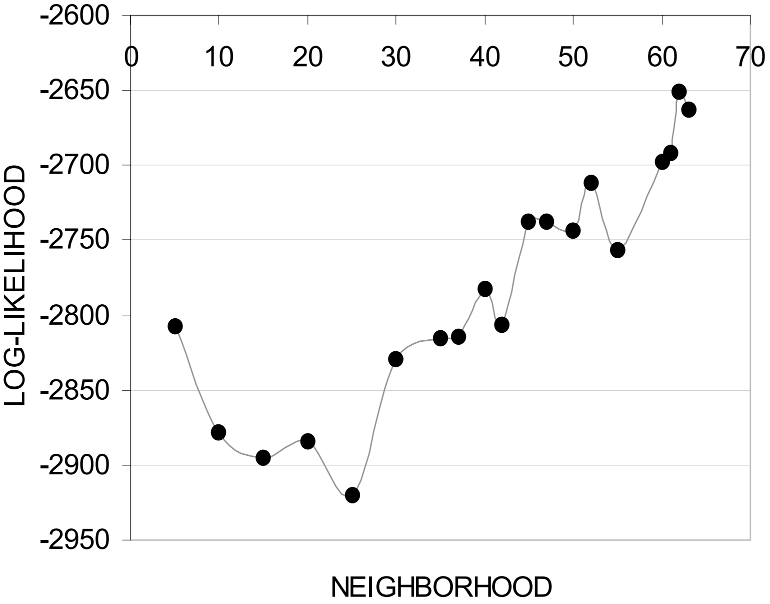

Figure 7.4. Log-likelihoods for null spatial linear models. The appropriate neighborhood accounting for spatial autocorrelation in bobwhite abundance was the neighborhood (in this case, $n = 62$) resulting in maximization of the log-likelihood.

function[5] incorporating polynomials of small grain field shape, sedimentary soil, and mean core area of woods, and single variables of the number of woods patches and variability in core area of row crop (Table 7.2; AICc = 5,062.3, adj-R^2 = 0.366). In occupied landscapes, small grain edge and proportion of the landscape in sedimentary soils were curvilinearly associated with greater relative abundance of bobwhite (Fig. 7.5). Bobwhite abundance also was positively associated with greater variation in the core area of row crop fields and negatively associated with number of woods patches and mean core area in woods.

Reduction of the model was not necessary as a smaller nested model containing each of the variables, except for number of wood patches and the square term for mean core area of woods, was less explanatory (AICc = 5,073.3, $U^2 = 10.9$, $P = 0.0009$). Residuals from the spatial linear model were homogenous and largely normal except for some (not significant) large positive values.

Importance of Small Grain Agriculture to Bobwhite

Small grain agriculture was important in both models of presence and abundance, prompting a closer examination of this relationship. I calculated mean and coefficient of variation in call counts for each NABBS survey stop from 1985–1998. I also calculated the proportion of occurrence and whether a stop was "at-risk" of extirpation. Proportion of occurrence was calculated as the number of years bobwhite were seen at a survey location in the 14 years of the study period, divided by 14. Areas of greater variability in

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[5] In the frequentist tradition, $U^2 = 238.0$, $P < 0.0001$.

Table 7.2. Influence of environmental parameters on relative Northern Bobwhite abundance in Illinois, as determined by North America Breeding Bird Survey data.

Parameter	β	SE	*t*	*P*
Intercept	0.7108	0.0205	34.66	<0.0001
Landscape Shape $\text{Index}_{\text{Small Grain, 5,000 ha}}$	0.9013	0.1382	6.52	<0.0001
Landscape Shape $\text{Index}^2_{\text{Small Grain, 5,000 ha}}$	-0.4875	0.1032	-4.72	<0.0001
Proportion Sedimentary $\text{Soil}_{\text{5,000 ha}}$	-0.1959	0.0794	-2.47	0.0137
Proportion^2 Sedimentary $\text{Soil}_{\text{5,000 ha}}$	-0.4089	0.0693	-5.90	<0.0001
Row Crop Core Area Coefficient of $\text{Variation}_{\text{500 ha}}$	0.0001	<0.0001	5.24	<0.0001
Number of Woods $\text{Patches}_{\text{5 ha}}$	-0.2750	0.0769	-3.58	0.0004
Mean Core Area/ Woods $\text{Patch}_{\text{50 ha}}$	-0.4302	0.0794	-5.42	<0.0001

Table 7.2. Continued.

Parameter	β	SE	*t*	*P*
Mean Core Area/ Woods Patch$^2_{50\ \mathrm{ha}}$	-0.1129	0.0648	-3.58	0.08

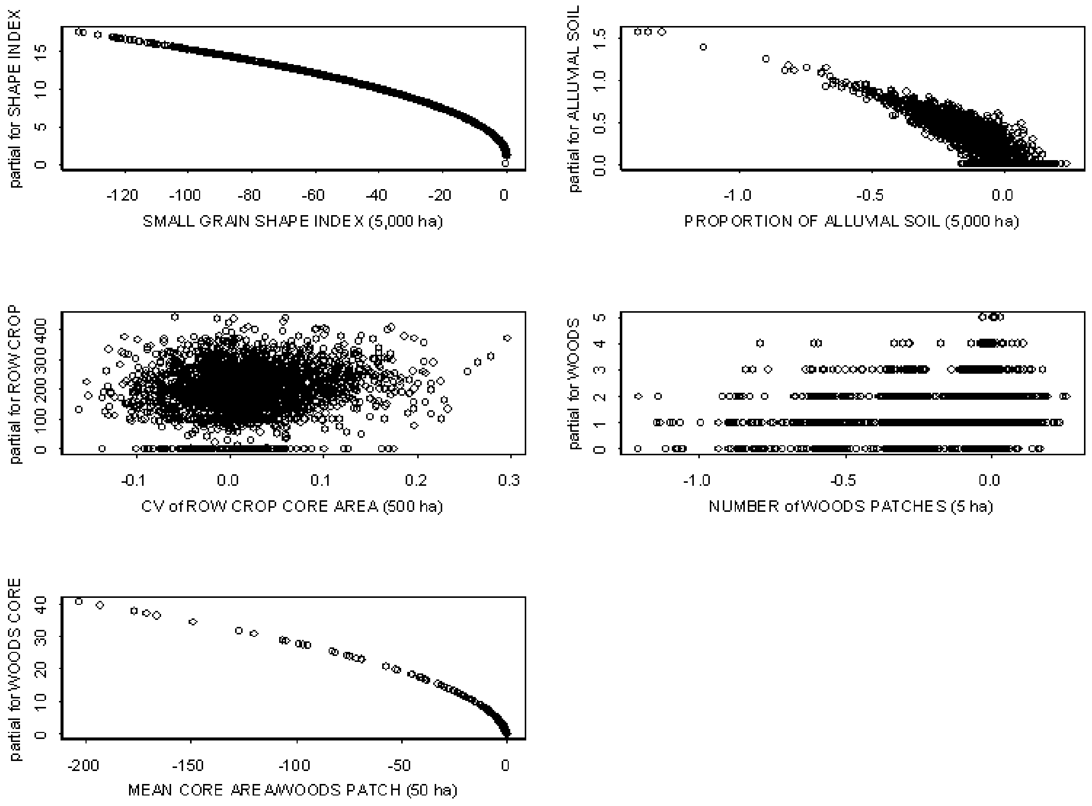

Figure 7.5. Partial regression plots demonstrating relative influence of environmental variables (see Table 7.2) on Northern Bobwhite relative abundance in Illinois, 1985–1998.

population abundance relative to the mean are more likely to proceed to extirpation than those exhibiting greater consistency. Thus, an at-risk site was defined as a stop where variance in bobwhite abundance exceeded mean abundance ($s^2/\bar{x} > 1$). Each of these metrics (mean, coefficient of variation, proportion of occurrence, and whether at-risk), because of their complementary nature, are useful population-level indicators of biological response. Areas with a high abundance of bobwhite in 1 year would be more likely to exhibit higher abundance of bobwhite in subsequent years, lowering the coefficient of variation and probability of extirpation, and increasing proportion of occurrence. Sites with low abundance would exhibit the opposite pattern, a lower proportion of occurrence, a potentially higher variation in number, and a greater risk of extirpation.

For NABBS call counts, I found bobwhite occurred at a lower frequency, in lower numbers, and with greater count variability when in wood habitats, whereas they occurred at the greatest frequency, at the highest numbers, and with less variability in small grain habitats (Fig. 7.6). Grassland and row crop habitats provided intermediate degrees of suitability in the local area about the survey location.

DISCUSSION

The wide geographic extent of regional bird monitoring programs usually makes avian-habitat use studies resulting from them largely non-experimental and exploratory in nature (Young and Hutto 2001). One goal of avian-habitat relationship studies is to identify environmental conditions controlling presence and abundance of a species. In this chapter, I identified complex associations between environmental conditions and bobwhite

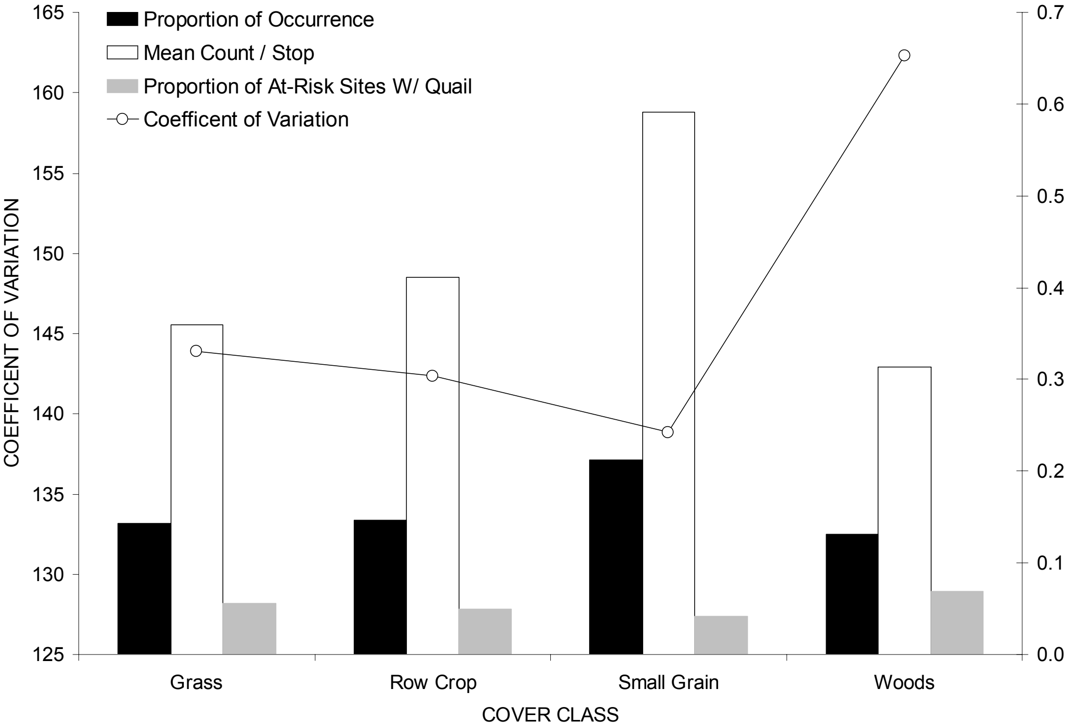

Figure 7.6. Proportion of occurrence, mean count per stop, proportion of sites with Northern Bobwhite at risk of extirpation, and coefficient of variation in bobwhite counts by land use / land cover class. Data are from the Illinois portion of the North American Breeding Bird Survey for 1985–1998.

presence and abundance. The final model of bobwhite presence included variables associated with landscape diversity, small grain agriculture, forest lands, and winter severity, whereas the final model of bobwhite abundance included indices of agriculture shape and size, soil characteristics, and forest land. The predominant scale at which quail were associated with landscape variables was 5,000 ha, the largest scale examined. Roseberry and Sudkamp (1998) reported significant associations between indices of bobwhite abundance and environmental variables at route and county scales. Their models, however, did not account for effects of spatial autocorrelation and did not consider environmental variables at small scales. Therefore, it is unclear as to which scale is ultimately most appropriate for measuring influences of landscape characters on bobwhite. Regardless, it does appear evident large scales produced the tightest associations with quail presence and abundance.

Presence

Model Results.—Bobwhite presence increased with increasing amounts of small grain and forest land use, and decreased with less landscape evenness and greater severity of winter weather. Bobwhite occurred more frequently in landscapes with 40% more small grain agriculture and 7% more woods than mean conditions; compared to landscapes devoid of bobwhite, landscapes with bobwhite had 118% more small grain agriculture and 54% more woodland.

Bobwhite presence increased as evenness approached the landscape mean. Landscape cover-type evenness increases with increasing landscape diversity and is described as the observed level of cover-type diversity divided by the maximum possible diversity (varying between 0 and 1). In Illinois, bobwhite were most highly related to intermediate values of evenness. Low levels of evenness would index landscapes with a lower amount of woods and small grain agriculture, reducing likelihood of occupancy. Conversely, high evenness suggests equal amounts of all cover types, including urban and suburban human habitation. Roseberry and Sudkamp (1998) concluded bobwhite were more highly associated with lower contagion in their Pattern-Recognition Model of Illinois bobwhite habitat; Ritter et al. (1995) reported a highly significant negative relationship ($r = -0.9$) between contagion (a configuration measure) and Shannon's J' (a composition measure), indicating the results of Roseberry and Sudkamp (1998) and this chapter concur.

Model Improvement.—Augustin et al. (1996) found autologistic regression, which accounts for spatial autocorrelation in a logit regression framework, produced a tighter fit to a known distribution than logistic regression alone. Given that model fit was high, correctly predicting >80% of validation data, little improvement may be made by accounting for spatial autocorrelation in distribution. There were, however, obvious deficiencies in model adequacy outside of the historical quail range. Therefore, additional model improvement may better resolve suitable habitat in those areas where bobwhite are sparsely distributed. My concern, though, is that landscape factors important in determining quail presence and abundance outside the historical quail range may differ substantially from those I identified based on threshold responses not accounted for in the linear approaches I utilized. Thus, further modeling, examining only those survey locations located in northern and eastern Illinois, may identify these different variables should they exist. Given that many of the mis-classified sites occurred along the northern periphery of the historical quail range, further modeling may benefit by including distance from the historical quail range as a covariate.

Additional model improvement may be possible if the cumulative effects of the late-1970s winters are incorporated in the model; as it was, I assessed only individual effects of climate. Some of the cumulative effects of weather were included by allowing the weather variables to be collinear, but this likely caused lower model goodness-of-fit. By the frequentist paradigm, variables reducing model goodness-of-fit should be excluded. Conversely, the Information Theoretic approach suggests assessments of final model goodness-of-fit are unnecessary given that the global model is properly fitted (Burnham and Anderson 1998:306). Burnham and Anderson (1998) indicated for models derived from large samples, goodness-of-fit for an AIC-defined final model is of little concern and that it is acceptable to use this model for inference. I appended the poorer-fitting model for those confident that Information Theory can more properly define the arena of inference (Appendix 7.C); regardless, β's for the landscape variables varied little between the 2 models.

Comparison to Other Landscape Models.—Schairer (1999) found bobwhite habitat suitability increased with the proportion of the landscape devoted to row crop and decreased as deciduous forest patch size increased. Burger et al. found similar results in that suitability increased with row crop shape index and density of woods edge. Since edge density is typically, though not always, negatively related to patch size, the authors of these 2 studies were generally in agreement. Burger et al. also reported a significant influence of Conservation Reserve Program (CRP) edge, which was not studied by Schairer (1999). Like my study, Schairer (1999) found very little of the Virginia landscape was highly suitable.

Abundance

Proportion of the landscape in sedimentary soils[6] negatively affected bobwhite abundance. These soils were thin (<100 cm) loess generally occurring on loam, Wisconsinan till, or lacustrine sediments. They were most abundant in the northeastern portion of the state, but were also commonly found scattered throughout southern Illinois. Guthery (2000:17) suggested loamy soils over limestone bedrock generally support high densities of bobwhite in north-central Texas; Guthery admitted, however, that the relationship between soil type, food abundance and diversity, and quail abundance has never been established. In Illinois, the negative effect of these loamy sedimentary soils on bobwhite abundance cannot be simply due to their agricultural importance since correlations between sedimentary soils and agriculture were generally small or negative. Rather, since sedimentary soils generally promote plant growth and the rate of succession due to their high nutrient content, these areas may lack sufficient open ground for bobwhite movement, constraining bobwhite abundance.

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[6] Soils identified as sedimentary included classes 6, 7, 8, and 9 of the parent soil material, as identified by Fehrenbacher (1982) and mapped by the Illinois State Geological Survey (1984).

Moderate to high values of landscape shape index for small grain agriculture were associated with higher numbers of bobwhite. This index is highly correlated with indices of edge abundance, indicating high amounts of small grain field edge in the landscape are important predictors of bobwhite abundance in Illinois.

Variation in row crop field size had a small, but positive effect; uniform field size, which would reduce this variation, was probably associated with modern ("clean") agricultural practices. These clean agricultural practices, primarily occurring in the agricultural plains of east-central Illinois, are associated with extremely large field size, negating their importance to bobwhite (Chapter 6).

As forest land increased in both abundance and number of patches, bobwhite declined in abundance, whereas moderate amounts of widely-distributed forest favored greater abundance. This finding concurs with that of Roseberry and Sudkamp (1998) and Guthery et al. (2001*b*), and disagrees with that of Brady et al. (1993). These contradictory findings may indicate a non-linear response of bobwhite to woods. In landscapes with little woods (e.g., Kansas), bobwhite seem to respond to increases in woody cover. In heavily wooded landscapes (e.g., western and southern Illinois), however, they respond negatively to further increases. This negative response of bobwhite abundance to woods amount should be tempered by the observation that increasing amounts of woods do promote bobwhite occurrence. Thus, clearly, while woody cover is necessary, (near) continuous woods act to depress bobwhite abundance. This negative response to continuous forest cover is likely due to a lack of openness at ground level. While dense forest understories are essential for winter cover (Roseberry and Klimstra 1984), too much likely precludes high abundance. For instance, Dixon et al. (1996) suggested bobwhite avoided pine woods in their South Carolina study area because a lack of the traditional grassy understory and invasion by midstory hardwoods reduced available food and cover. Bobwhites neither scratch strongly in leaf litter nor maneuver easily through thick brush.

Guthery et al. (2001*b*) claims to have disproven Leopold's Law of Interspersion (Leopold 1933), the positive association of bobwhite with land cover edge, by reporting an instance in which bobwhite were not positively associated with edge; they suggested 1 instance is all that is necessary to invalidate an ecological theorem. However, only 2 paragraphs earlier in their paper they indicated associations between bobwhite and habitat were context dependent. It seems in the context of the Illinois landscape, bobwhite do respond favorably to the amount of 1 type of edge, that of small grains. Thus, I disagree with Guthery et al. (2001*b*) and suggest previous counter instances in which bobwhite were either not associated or negatively associated with edge must also be interpreted within the context of the particular landscape in which the study was conducted. In some contexts, bobwhite do respond to landscape edge and, therefore, it is premature to suggest Leopold was entirely wrong.

This context-dependent association of bobwhite to landscape features needs better understanding. The form of the relationship between bobwhite response and varying amounts of land use practices is not clear. I offer a graphical model as a starting point for defining the slope, shape, and range of the relationships of bobwhite to various land use practices (Fig. 7.7).

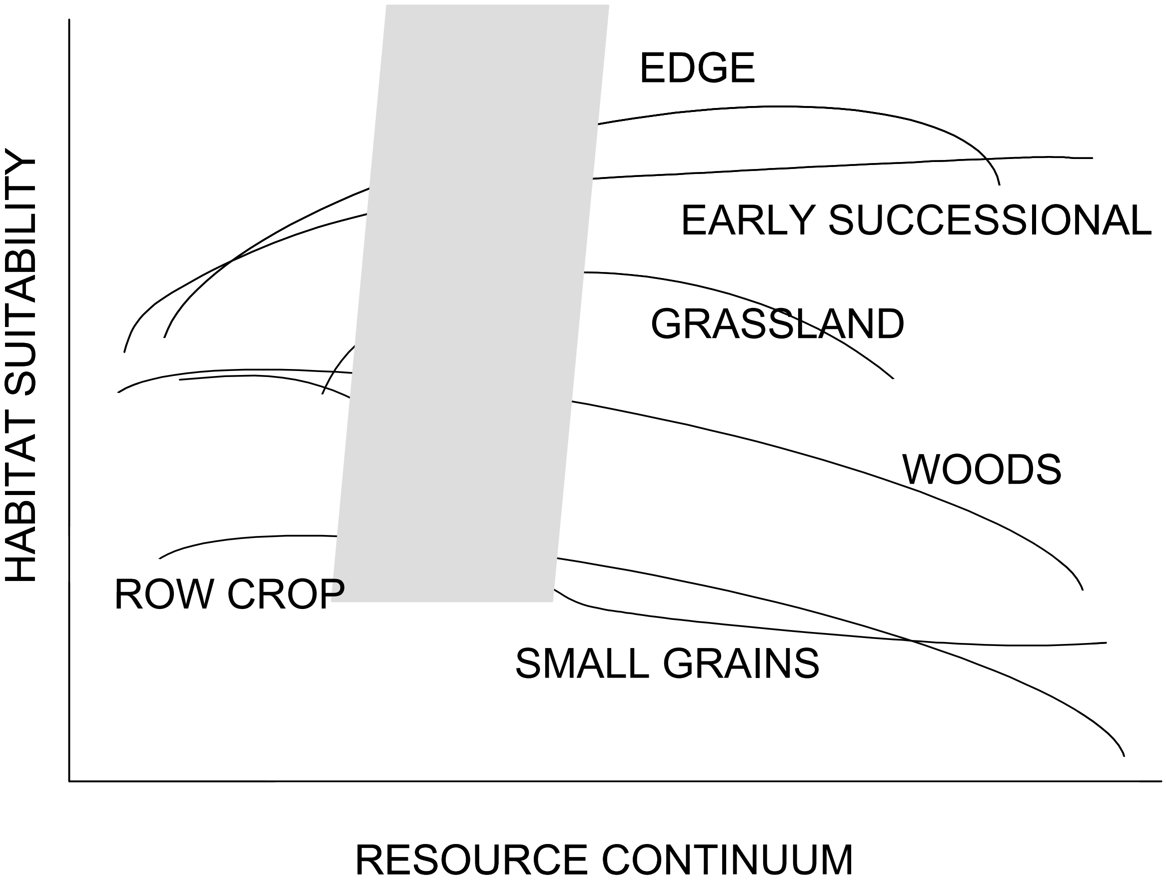

Figure 7.7. Theoretical relationships of Northern Bobwhite to various land use/land cover classes. The relative positions, range, and slope of the relationships are currently unknown. The gray parallelogram represents a theoretical optimal configuration of the land cover classes for bobwhite in Illinois.

Potential Bobwhite Population Size in Illinois

Brennan (1999) suggested fall quail densities on high-quality habitat ranged between 2.2 and 4.4 birds · ha^{-1} whereas Leopold (1933) reported bobwhite density rarely exceeded 2.5 birds · ha^{-1} in the agro-environs of the Midwest. For 71,294 km^2 of suitable habitat in Illinois, these density estimates translate to 15,684,680 quail at 2.2 birds · ha^{-1}, 23,527,020 quail at 3.3 birds · ha^{-1}, and 31,369,360 quail at 4.4 birds · ha^{-1}. These estimates are undoubtedly too high. Figure 7.2 suggests little, if any, high-quality landscape-scale habitat exists in Illinois. Thus, based on Preno and Labisky's (1971) late winter estimate of 0.2 birds · ha^{-1}, measured when bobwhite were at their apex of abundance in Illinois, the number of bobwhite in Illinois may only be ~1,425,880. This is a pre-breeding estimate, which is often only about 35% of the fall population size. If this ratio is reasonable fall population may number 4 million. Current estimates of annual harvest are ~500,000 birds · yr^{-1}, or about 1/8 of this estimated total population size. Both the pre-breeding and fall estimates of population size exceed the population goal (921,600) set forth by the Northern Bobwhite Conservation Initiative (NBCI; Southeast Quail Study Group Technical Committee 2001). These estimates of population size are probably upper limits to the true population size, given that land within suitable landscapes differs in their site-level suitability. Given that annual harvest is currently ~500,000, >15% of each landscape must comprise suitable sites. The NBCI assumed ⅓ of the fall pre-hunt population was removed by harvest, which would indicate the true fall population is 1.5 million. This translates to a hypothesis that 37.5% of each suitable landscape is adequate site-level bobwhite habitat.

Small Grain Agriculture

Even though small grain agriculture comprised <6% of the Illinois landscape, it was very important in determining both bobwhite presence and abundance. Because bobwhite occurred at their highest abundance, varied least in abundance, probability of occupancy was greatest, and risk of extirpation was lowest in areas of small grain agriculture it is doubtful if the association of bobwhite with small grain agriculture is spurious. In Illinois, small grain agriculture included winter and spring wheat, winter rye, winter and spring oats, triticale, and winter and spring barley (Nafziger 2001). By far, the most common small grain crop was soft red winter wheat, a low protein and gluten variety useful in baking and gum production (Nafziger 2001).

Robel et al. (1979) reported both corn and soybean (row crops) and western ragweed (found in grasslands) provided ~25% more usable energy than wheat. Thus, it is doubtful the importance of small grain agriculture to bobwhite is due solely to the value of small grain seeds to bobwhite energetics. However, small grain waste, unlike the more energy-packed row crops, is readily available at a time of the year when corn and soybeans are not, during spring and early summer. Winter wheat is planted in late September and October. After initial growth, the wheat is dormant through winter until growth resumes in late winter (March). Wheat begins to head in early May and harvest occurs in June and July. Nearly 14%, or 80,000 ha, of the annual Illinois small grain crop is left unharvested (Nafziger 2001). This growth pattern may make waste grain more accessible to bobwhites, especially early in the nesting period. Small grain cultivation may also produce heavy stands of native annuals such as ragweed (*Ambrosia* spp.), *Croton* spp., and wild legumes (Stanford 1980) and abundant insects (Palmer et al. 1992) which also rate high as quail food.

Wheat fields probably undergo less disturbance during the early breeding period than fields planted in corn or soybeans. While application of fertilizers and herbicides to wheat fields typically occurs in late winter (March), there is a 10-week period afterwards where the fields are left to grow. Concurrently, soybean and corn fields planted in late April and early May produce a tremendous disturbance when bobwhite begin breeding. This combination of timely seed availability and lack of human disturbance may account for the positive response of bobwhite in areas of small grain agriculture in Illinois.

Small grain fields may also provide important nesting or brood-rearing area (Southeast Quail Study Group Technical Committee 2001). Gray Partridge have been found to nest in oat fields (Allen 1984) and Warner (1984) reported that Ring-necked Pheasant broods in Illinois used oats, hayfields, and cultivated rowcrops. Although oats and hayfields constituted only 6.4% of their study area (similar to the percentage across the state), Warner (1979, 1984) noted ~½ of all radiotelemetry locations for broods ≤4 weeks old were in those 2 cover types. Either an oat field or a hayfield served as the primary focus of activity for all broods. Broods from hatch to 9 weeks of age occupied 17.8 ha in oat- and hayfield-dominated landscapes and 22.3 ha in rowcrop-dominated landscapes, suggesting the former were of higher quality (Warner 1984). Corn and soybeans were considered of little value to pheasant chicks as foraging habitat because of their low insect abundance and biomass (Warner 1979, 1984).

Finally, it might be reasonable to presume that small grain agriculture may provide important additional winter cover not available in areas dominated by row crop agriculture. Wheat begins to tiller (shoots sprouting from the base of a grass) 3–4 weeks after initial growth and subsequently prior to dormancy in November. Graber and Graber (1963) described winter wheat in Illinois as relatively short (7–13 cm, versus a bobwhite standing 20 cm) and dense with bare soil only between rows. Early formation of shoots and the overhead cover that fall growth provides may produce accessible winter foraging areas[7]. Gray Partridge are often seen having pushed through a light covering of snow atop winter grains to expose the waste grain below (Allen 1984); bobwhite may exhibit similar behavior. Previous studies by Graber and Graber (1963), however, suggest winter use by quail has been limited historically. Graber and Graber (1963) reported avian use of agricultural habitat in the early- and mid-1900s. They found winter quail densities in small grain stubble fields varied between 0.05 birds$\cdot$ ha^{-1} in the north and 0.50 birds$\cdot$ ha^{-1} in the south, but only in 1906–1907, not 1956–1958. In no years did they observe quail in soybean stubble fields, plowed fields, or harvested wheat fields, but they did observe use of corn fields harvested by hand in 1906. It appears agricultural fields provide little in the way of usable space in winter, but when agricultural fields are used, they are generally in small grain production.

That small grain agriculture is important to bobwhite in Illinois is contrary to the results of Brady et al. (1993) for Kansas. They reported a negative association of bobwhite with both oats and wheat. Wheat, however, was the predominant agricultural

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[7] Many winter wheat varieties are prostrate or “creeping” prior to dormancy, so the value of winter wheat to overhead cover may be questionable, at least depending upon the variety under cultivation.

practice in Kansas, indicating the relationship of bobwhite with small grains may be curvilinear. Where this possible apex occurs is unknown, but must lay between the 6% of the landscape in Illinois and the ~58% in Kansas devoted to small grain agriculture.

Roseberry and Sudkamp (1998)

The Roseberry and Sudkamp (1998) model of bobwhite suitability predicted suitable landscapes after accounting for inclement weather; they approximated the risk of annual winter severity through their use of latitude. My initial model of landscape suitability did not incorporate this winter severity in defining suitable landscapes; subsequent models, however, incorporated historical winter severity (Appendix 7.C).

My model of bobwhite suitability predicted 64% more available habitat than the model of Roseberry and Sudkamp (1998) (72,261 km^2 vs 35,000 km^2), principally due to a more patchy configuration in the Roseberry and Sudkamp (1998) map. Suitable habitat in both models was distributed throughout the west-central and southern portions of the state, in the traditional quail range (81% agreement between models). My model also predicted a greater amount of suitable habitat in the Wisconsin Driftless section in the northwest portion of the state and in the Kankakee Plain south of Chicago.

I believe the means by which Roseberry and Sudkamp (1998) mapped suitable habitat may have been inappropriate. My approach predicted more suitable habitat because variables found to be important were generally measured and mapped at the largest scale, 5,000 ha. The Roseberry and Sudkamp approach, however, while measuring suitability based on route (area range = 173–270 km^2) and county (area range

= 430–2,965 km^2) scales, mapped these variables for 9 0.09-ha pixels based on calculations conducted for 2.6-km circles (~2,100 ha) around the focal cell. Mapping of significant large-scale associations at small scales undoubtedly leads to a patchier distribution of suitable habitat. This would be safe to do if their results were scale invariant, but as I have demonstrated, this lack of variance across scales was unlikely (Wiens 1981).

The map I developed defines the landscape-level conditions within which bobwhite occur as viable populations. Outside of these defined areas, bobwhite are likely occurring as remnant populations with only short times to extinction. Site-level conditions will play an immense role in determining the particular presence and abundance of Northern Bobwhite, skewed by the influence of larger scale landscape processes that I have identified. Higher-scale models cannot correctly determine if bobwhite will occur in suitable landscapes unless landscape variables are correlated with site characters.

CHAPTER EIGHT

INFLUENCE OF POPULATION STRUCTURE ON PERSISTENCE PROBABILITY

Patches of seemingly suitable habitat may not be occupied if they are too distant from occupied patches. Distant patches would likely experience less immigration from neighboring patches, which may be important for population persistence. These ideas of population persistence aided by dispersal from neighboring populations are embodied in the emerging metapopulation paradigm.

Wells and Richmond (1995:461) provided the following criteria to identify a metapopulation:

> “If individuals breed in >1 spatially disjunct group during a breeding season, the groups should be considered a single population spread over a patchy habitat. If individuals breed within a single spatially disjunct group during a breeding season, but some breed in a different spatially disjunct group in another breeding season, the groups should be considered a set of populations making up a population.”

In a metapopulation, small populations are prone to extirpation, with recolonization occurring only by dispersal of individuals from adjacent populations (Hanski and Gilpin 1997, Hanski 1999). Populations occurring within habitat patches within the dispersal distance of a bobwhite likely exist as a metapopulation. Those patches not accessible through dispersal likely act as distinct and separate populations.

There are numerous means by which to evaluate metapopulation dynamics. Hanski (1994*a*,*b*; 1999) developed the Incidence Function Method (IFM) to model persistence and extirpation of populations within metapopulations. The simplicity of this approach is appealing in that all it requires to fully parameterize the model is information regarding patch size and location and occupancy status of patches. A single census of available patches is usually sufficient to parameterize the model.

Unfortunately, my data preclude the use of this method since I do not have reliable patterns of individual patch occupancy. However, I do have information regarding patterns in population extirpation and recolonization (Chapter 5). Sjögren-Gulve and Ray (1996) outlined a procedure whereby it is possible to model metapopulation dynamics with information regarding population state transitions. Unlike the IFM, this approach allows for multiple environmental factors to govern colonization and extinction (Sjögren Gulve 1994).

I used the Sjögren-Gulve and Ray (1996) approach to discern environmental factors associated with population state transitions. Because my use of the approach of Sjögren-Gulve and Ray (1996) was not completely successful, I also implemented a mechanistic model incorporating aspects of bobwhite demography to predict state transitions. My hope was that these approaches would provide insight into the among-population dynamics of bobwhite. The questions I asked were: what habitat variables govern population-state transitions? Do empirical data indicate a metapopulation approach is valid for management purposes?

METHODS

Connectivity Between Populations

To determine likelihood of movement by bobwhite between patches, I reviewed and summarized all available studies documenting bobwhite dispersal movements. The proportion of and distances moved by bobwhite were summarized and plotted. A 3rd-order polynomial was fitted to $\log_{10}$-transformed distance (log(DISTANCE[m])).

As a check against the hypothesized dispersal function, I calculated median and maximum dispersal distances based on taxa-specific scaling equations provided by Sutherland et al. (2000). These equations are:

$$2.1\ (\pm\ 1.76) \cdot M^{0.18\ (\pm 0.18)}$$

for median dispersal, and

$$36.4\ (\pm\ 1.55) \cdot M^{0.14\ (\pm 0.15)}$$

for maximum dispersal. Body mass (M) was set to 0.1782 kg (Roseberry and Klimstra 1971).

Delineating Population Structure

Optimal habitat was defined as a combination of small grain agriculture, woods, elevation, and landscape evenness (Chapter 7). This raster model was dichotomized at an HSI = 0.5, with an HSI $\geq$ 0.5 identified as potentially suitable habitat and an HSI < 0.5 identified as matrix (inhospitable) habitat. Based on this discretization of habitat, habitat patches were delineated with the region group command in PatchGrid. The *buffer* command in ArcInfo 8.0 (Environmental Systems Research Institute, Redlands, California) was used to buffer each habitat patch by the typical maximum dispersal distance for bobwhite. Patches within the coalesced buffer were identified as forming a single network of habitat. Individual networks were indentified, and the number and size of patches per network calculated. Patches <4 ha were deleted from the networks as this was the approximate lower limit of habitat necessary to sustain a covey of bobwhite at this latitude (Kansas, Robinson 1957*b*; Illinois, Bartholomew 1967; Iowa, Crim and Seitz 1972; Illinois, Urban 1972; Tennessee, Yoho and Dimmick 1972).

Modeling Patch-State Transitions

As in Chapter 7, logistic regression was used to relate environmental variables to a dichotomous response. In this instance, the responses examined were a transition from occupied to extirpated (extinction), and from unoccupied to occupied (colonization) (Sjögren-Gulve and Ray 1996). The data used were Illinois Department of Natural Resources call counts because they offered a robust measure of turnover probability (Chapter 4).

Identifying Candidate Variables.—Candidate variables were identified with Somers' D rank correlation and the C statistic. Somers' D is an ordinal measure of association where *x* predicts *y*, varying between -1 and 1. This measure is basically the equivalent of Pearson's product-moment correlation for linear regression. The C statistic is a summary measure for the Receiver Operating Characteristic (ROC) curve (Hanley and McNeil 1982), which evaluates model discrimination. This ratio has a value from 0–1, with 1 being perfect predictive value, 0.5 being no predictive value, and 0 being perfect negative predictive value. A C >0.7 is acceptable, >0.8 is good, and >0.9 is excellent (Margolis et al. 1998).

Model Determination.—A full model was created at each of 3 scales (50-, 500-, and 5,000-ha), containing variables with D > 0.12 and C > 0.55. Multicollinearity was assessed and the less explanatory of the collinear variables were removed. The new full model was then subjected to a stepwise procedure whereby variables were removed and added and evaluated at each step by their Aikike's Information Criterion score.

Variables from the final scale-specific models were included in a new final model and the process of variable reduction was continued. Significance of the variable to stay was set at $P < 0.10$.

Goodness-of-Fit.–Goodness of fit was assessed in 2 ways, with the Brier score and the C-H-C-H goodness of fit test. The Brier score is the mean of the mean squared error between the predicted and observed events. Scores vary between 0 and 1, with a more accurate model closer to 0. A model agreeing with the known outcome 50% of the time has a score of 0.25.

Patch Turnover Probabilities: Modeling Metapopulation Dynamics

Environmental variables defined by logistic regression as important in determining patch extinction and colonization were used to calculate turnover probabilities based on the mean condition of observed patches. Sjögren-Gulve and Ray (1996) suggested a high model goodness-of-fit was essential for their approach to work adequately. Since final model results were statistically sound, but did not attain the goodness-of-fit suggested by Sjögren-Gulve and Ray (1996) ($P > 0.9$), I assessed a third approach. Sachot (2000) developed a spatially-explicit population viability analysis program (TetrasPool 1.0.2) specifically for galliforms. The model has been successfully applied to predicting Capercaillie and Hazel Grouse metapopulation persistence. The model integrates demographic characteristics, dispersal behavior, and spatial characteristics of individuals within populations to determine individual- and meta-population persistence. Since population-specific parameters were not available, mean or typical demographic conditions were derived from a review of the literature (Table 8.1). These mean demographic conditions were altered to reflect the slight downward trend in abundance observed since 1981 (Chapter 3).

Population settings included geographical position (Easting and Northing), initial population abundance, and carrying capacity. Initial population abundance was established as 0.2 birds $\cdot$ ha^{-1}, whereas carrying capacity was set at twice as high (0.4 birds $\cdot$ ha^{-1}; equivalent to 1 bird $\cdot$ ac^{-1}) (Preno and Labisky 1969). Female home range size and overlap, which determines habitat packing and whether dispersal occurs between populations rather than within populations, were set to 12 ha and 45%, respectively. Dispersal was allowed to proceed in random directions. Migration rate was set to 0.1, based on migration rates observed for Rock Partridge (*Alectoris graeca saxatilis*; Cattadori et al. 2000). Cattadori et al. reported high dispersal rates for Rock Ptarmigan (*Lagopus mutus*) and Black Grouse ($\delta = 0.29$ and 0.25, respectively), and low dispersal for Capercaillie and Hazel Grouse ($\delta = 0.15$ and 0.14, respectively). For the relatively sedentary Rock Partridge, $\delta = 0.09$.

Table 8.1. Demographic conditions used in simulations of population performance and resultant fundamental net reproductive rate (λ). The implemented conditions were the particular parameter values used in the mechanistic metapopulation model.

Demographic Parameter	Typical Observed Condition	Implemented Condition
Proportion of females producing chicks	0.40[1]	0.52
Clutch size	12[2]	13
Sex ratio	0.40[3]	0.42
Annual adult survival rate	0.20[4]	0.27
Annual juvenile survival rate	0.20[4]	0.25
$\bar{x}_{\text{dispersal}}$ for a juvenile female (m)	NA	1,540[5]
Migration rate δ	0.1	0.1
λ	0.584	0.980

[1] Burger et al. (1995*b*)
[2] Stoddard (1931:39), Klimstra and Roseberry (1975:19)
[3] Roseberry and Klimstra (1984)
[4] Pollock et al. (1989), Burger et al. (1995*a*)
[5] From this study

Both environmental and demographic stochasticity were allowed to occur. Environmental stochasticity affected the proportion of females producing chicks, juvenile and adult survival rates, and clutch size. Demographic stochasticity influenced individual reproductive, survival, and fecundity statuses. Simulations were conducted for 100 time steps, and replicated 1,000 times.

RESULTS

Dispersal Probability Function

Fifteen studies reported movement distances (Table 8.2); 7 studies reported data regarding the number of bobwhite and their associated dispersal distance. Most studies suggested mean dispersal was rarely >0.5 km, and maximum dispersal typically <2.0 km. Three studies reported a few lone bobwhite dispersing 14–17 km; Duck (1943) reported a single bobwhite moving nearly 42 km across Oklahoma until it came to rest at the first tree it spotted.

A residual plot of the dispersal probability function suggested an unexplained pattern in the data, so splines, using a smoothing parameter $\lambda = 0.01$, were fitted to the plot to increase descriptive ability. Bobwhite dispersal movements suggested 95% of bobwhite disperse <2 km and 98% disperse <3 km (Fig. 8.1). From Sutherland et al.'s (2000) equations, bobwhite in Illinois were hypothesized to disperse a median distance of 1.54 km (range = 0.34–2.07 km) and a maximum distance of 35.34 km.

Table 8.2. Mean and maximum movements (km) observed in bobwhite.

Location	Distance Traveled (km)		Study
	Mean	Maximum	
Iowa	2.4		Errington (1933)
northwestern Oklahoma	15.6	41.8	Duck (1943)
Oklahoma	0.2-2.6	14.1	Baumgartner (1944)
southwestern Texas	0-10.6	16.9	Lehmann (1946)
central Missouri	0.5	0.8	Murphy and Baskett (1952)
Iowa		5.6	Boehnke (1954)
central Missouri		0.8	Lewis (1954)
central Missouri	0.1-0.6	2.0	Agee (1957)
Florida		15.3	Loveless (1958)
southern Illinois	0.2	0.6	Roseberry (1964)
Indiana		8.2	Hoekstra and Kirkpatrick (1972)
southern Illinois		2.0	Urban (1972)
Oklahoma	0.4		Yoho and Dimmick (1972)
Florida/Georgia	0.2	1.5	Smith et al. (1982)
southern Illinois		1.0	Roseberry and Klimstra (1984)

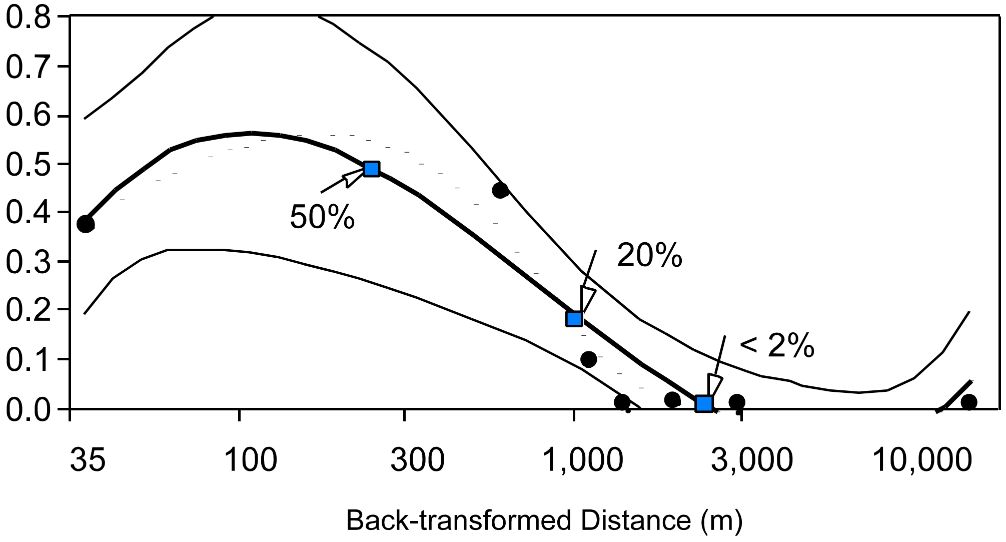


Figure 8.1. Dispersal probability function derived from reported bobwhite dispersal movements. The black line is a polynomial (95% CI) fitted to the observed values.

State-Transitions

Calculation of Somers' D (Table 8.3) indicated extinction and colonization transitions were most highly correlated with configuration variables measured at the 5,000-ha scale, such as Mean Core Area per Patch (MCA1) in the landscape and Mean Area per Disjunct Core (MCA2) of woods habitat. However, no variable alone was adequate (C > 0.70) in describing differences in either colonization or extinction transitions.

The final model describing colonization transition probabilities incorporated Total Core Area Index and Mean Core Area Index of Woods, both at 5,000 ha, and Core Area of Woods at the 50-ha scale (Table 8.4). While the colonization model described a significant portion of the variance in colonization probability (L.R. $\chi^2_5 = 100.7$, $n = 1{,}048$, $P < 0.0001$) and was sufficiently well-fitted (Brier = 0.225; C-H-C-H goodness of fit $Z = -0.593$, $P = 0.55$), general model performance was relatively poor (Nagelkerke $R^2 = 0.123$, C = 0.664, Tau-a = 0.162). All 3 diagnostics (R^2, C, Tau-a), along with the odds ratios, indicated a model performing somewhat better than chance. Interpretation of R^2 is straightforward. A C = 0.664 indicated a randomly selected colonization event will be assigned a higher predicted probability by the logistic regression model than an event of continued absence nearly 66 times of 100. Tau-a = 0.162 indicated a poor correlation between predicted and observed observations.

Partial residual plots indicated a great degree of overlap between colonization (1) and continued absence (0), but at the high end of the distributions (e.g., a TCAI > ~60, an MCAI > ~10, and a CLAND > 20) colonization was highly favored. Odds ratios

Table 8.3. Somers’ D rank correlation (D) between colonization or extirpation event and selected scale-specific environmental variables. The value for C is the proportion of times a randomly selected positive event (1) has a test value greater than that for a randomly chosen null event (0); proportions equal to 0.5 indicate no difference between positive and null events. Sample size was large ($824 \geq n \geq 1{,}048$) in all cases.

Environmental Variable	Scale (ha)	Colonization/ Extirpation	D	C
MCA1 (Landscape)[#]	5,000	Colonization	0.2464	0.6232
MCA2 (Woods)	5,000	Colonization	0.2416	0.6208
TCAI (Landscape)	5,000	Colonization	0.2334	0.6167
Woods Area	50	Colonization	0.1801	0.5900
MCAI (Woods)	5,000	Colonization	0.1693	0.5846
MNN (Landscape)	5,000	Colonization	0.1625	0.5812
MCAI (Grass)	5,000	Extinction	0.1974	0.5987
Mean Grass Patch	5,000	Extinction	0.1422	0.5711
IJI (Row Crop)[#]	5,000	Extinction	0.1350	0.5675

[#] Also, correlated with extirpation and colonization.

Table 8.4. Results of logistic regression of colonization probabilities and environmental variables. TCAI is Total Core Area Index, MCAI is Mean Core Area per Patch, MNN is Mean Nearest Neighbor, and MPI is Mean Proximity Index.

Variable	β	SE	Wald Z	*P*	Odds Ratio (CI)
Intercept	-5.595	1.141	-4.90	<0.0001	
$\mathrm{TCAI}_{5,000\ \mathrm{ha}}$	0.035	0.006	5.66	<0.0001	1.036 (1.023–1.048)
$\mathrm{MCAI}_{\mathrm{Woods},\ 5,000\ \mathrm{ha}}$	0.060	0.026	2.30	0.0214	1.061 (1.009–1.116)
$\log(\mathrm{MNN}_{\mathrm{Row\ Crops},\ 5,000\ \mathrm{ha}}+1)$	1.661	0.566	2.94	0.0033	5.264 (1.737–15.950)
$\log(\mathrm{Woods\ Area}_{50\ \mathrm{ha}}+1)$	0.536	0.159	3.36	0.0008	1.709 (1.250–2.335)
$\log(\mathrm{MPI}_{50\ \mathrm{ha}}+1)$	0.385	0.228	1.69	0.0907	1.469 (0.941–2.295)

indicated a 1 unit change in TCAI would affect a 4% change in probability, whereas a 1 unit change in MCAI would affect a 6% change. A change of 1 unit, log-transformed, in MNN would affect the largest change, nearly 526%; however, the transformation confounds interpretation of the true odds.

Models of extinction fared little better (Table 8.5). This time, however, 2 candidate models were resolved with nearly equal discriminatory ability. Model 1 included terms for interspersion and juxtaposition of small grain agriculture, mean area per disjunct core of grassland, a landscape measure of core area, and human influence in the landscape (Table 8.5). Human habitation in a 500-ha area was highly related to the amount of core woods in a 50-ha area ($r = 0.96$). Thus, Model 2 differed from Model 1 in that it replaced $\text{Human}_{500\text{ ha}}$ with $\text{CLAND}_{\text{Woods, 50 ha}}$. The core area index for the landscape was not significant in this second model and was dropped. Aikike's Information Criterion was similar for the 2 models (Model 1: 43.02, Model 2: 44.11, ΔAIC = 1.09). AIC weights indicated Model 1 was favored as the model closest to truth (0.633 vs 0.367). While both models were well-fitted (C-H-C-H Z's < -0.68, *P*'s > 0.39), they discriminated poorly between transitions to extinction and continued persistence (C's = 0.621, Tau-a = 0.121, $R^2 = 0.06$). The Brier score, a measure of both fit and discrimination, was 0.237 for each model, indicating the models performed barely better than chance. This poor model fit precludes successful implementation of the Sjögren-Gulve and Ray (1996) approach to modeling metapopulation dynamics; they suggested model fit must be very good to successfully proceed.

Table 8.5. Competing logistic regressions of extirpation probabilities and environmental variables. MCA2 is Mean Core Area per Disjunct Patch, IJI is Interspersion and Juxtaposition Index, MCAI is Mean Core Area per Patch, and CLAND is Amount of Core Area. All variables were transformed except for IJI. Transformation was $\log_{10}$ except for CLAND, which was arcsin-square root transformed.

Variable	β	SE	Wald Z	*P*	Odds Ratio (CI)
Intercept[a]	-2.319	0.448	-5.17	<0.0001	
$\text{MCA2}_{\text{Grass, 5,000 ha}}$	1.582	0.358	4.42	<0.0001	4.867 (2.412–9.820)
$\text{IJI}_{\text{Small Grains, 5,000 ha}}$	0.017	0.007	2.48	0.0132	1.017 (1.004–1.031)
$\text{MCAI}_{\text{5,000 ha}}$	0.561	0.336	1.67	0.0944	1.753 (0.908–3.385)
$\text{Human}_{\text{500 ha}}$	11.058	4.506	2.45	0.0141	63,475 (9.3–>4
Intercept[b]	-2.142	0.428	-5.00	<0.0001	
$\text{MCA2}_{\text{Grass, 5,000 ha}}$	1.708	0.348	4.90	<0.0001	5.519 (2.789–10.924)
$\text{IJI}_{\text{Small Grains, 5,000 ha}}$	0.019	0.007	2.79	0.0053	1.019 (1.006–1.033)
$\text{CLAND}_{\text{Woods, 50 ha}}$	1.638	0.548	2.99	0.0028	5.142 (1.758–15.039)

[a] Model 1

[b] Model 2

Population Structure

An ArcView shapefile created from the limiting habitat grid layer revealed 416 patches of habitat >4 ha occurring in 52 networks (Fig. 8.2). Available habitat was dominated by 1 patch equaling 6,998,666 ha, 91% of all habitat. Minus this "mainland" patch, mean patch size was 1,851 ha (SE = 97 ha); the median, however, was 32 ha. Patches ≥1,000 ha ($n = 56$) comprised 647,409 ha, or 8% of potential habitat (Fig. 8.3*a*).

A contour surface depicting distance between patches of optimal landscape habitat was created. This analysis suggested virtually no patch in Illinois was >17 km from another suitable patch of optimal habitat, the approximate maximum dispersal distance for bobwhite (Fig. 8.1). Only when contours of 2 km were established were significant numbers of patches isolated from one another. In general, population networks possessed ≤5 patches (Fig. 8.3*b*). Only 1, the network containing the "mainland", consisted of >100 patches.

Metapopulation Persistence

Given the configuration of the mechanistic model, no individual or meta-populations were predicted to persist beyond a century ($\bar{x} = 21.0 \pm 1.8$ yrs, range = 3–56 yrs). Not surprisingly, metapopulation persistence was most highly related to initial population size of the metapopulation (Table 8.6, $F_{2, 44} = 1{,}367$, $R^2 = 0.98$, $P < 0.0001$), indicating larger initial populations lasted longer. Number of neighbors in a metapopulation contributed a small, but significant, positive amount to the explained variance.

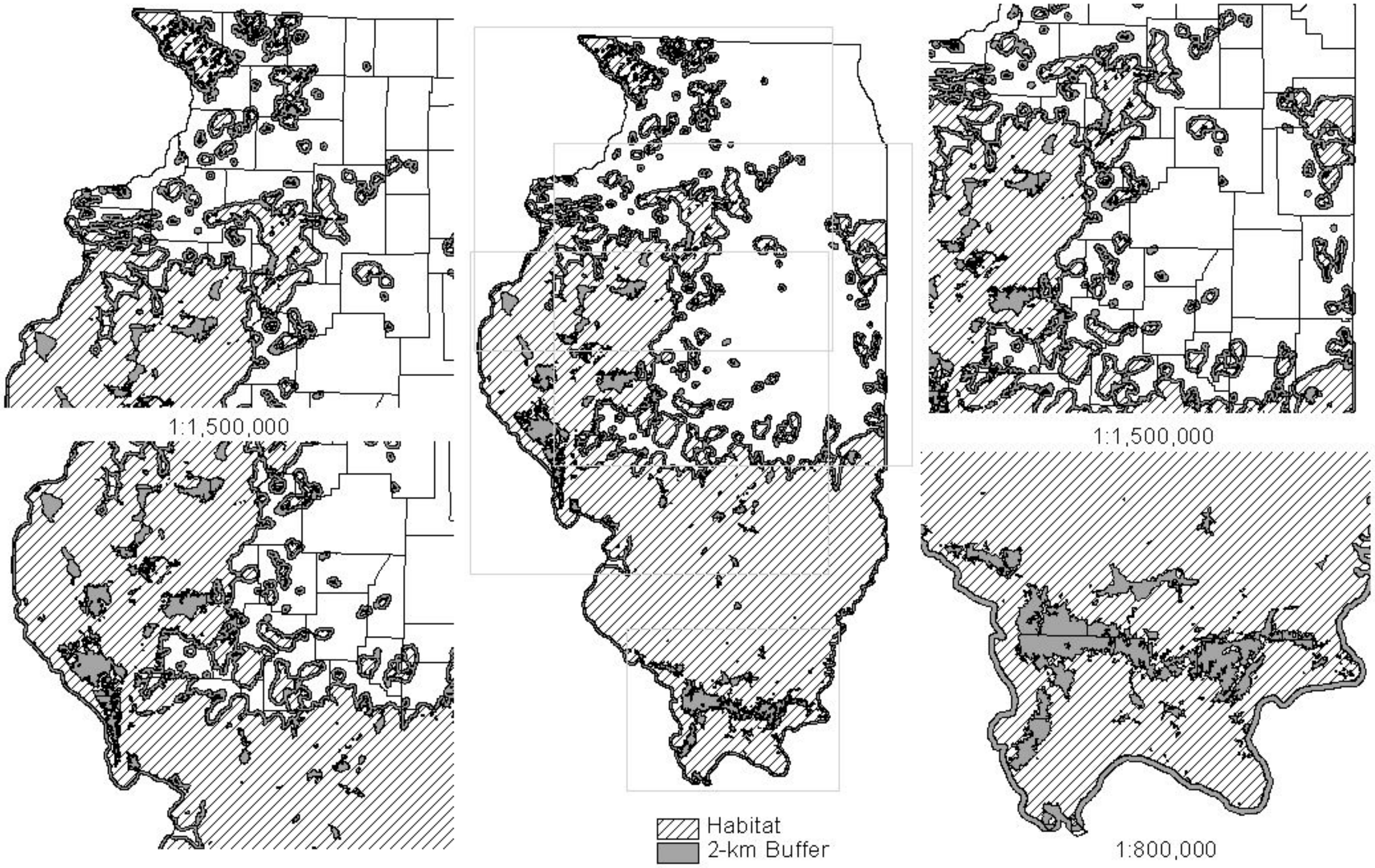


Figure 8.2. Potentially suitable Northern Bobwhite habitat in Illinois delineated into unique metapopulations by a 2-km buffer representing the typical maximum dispersal distance of the species.

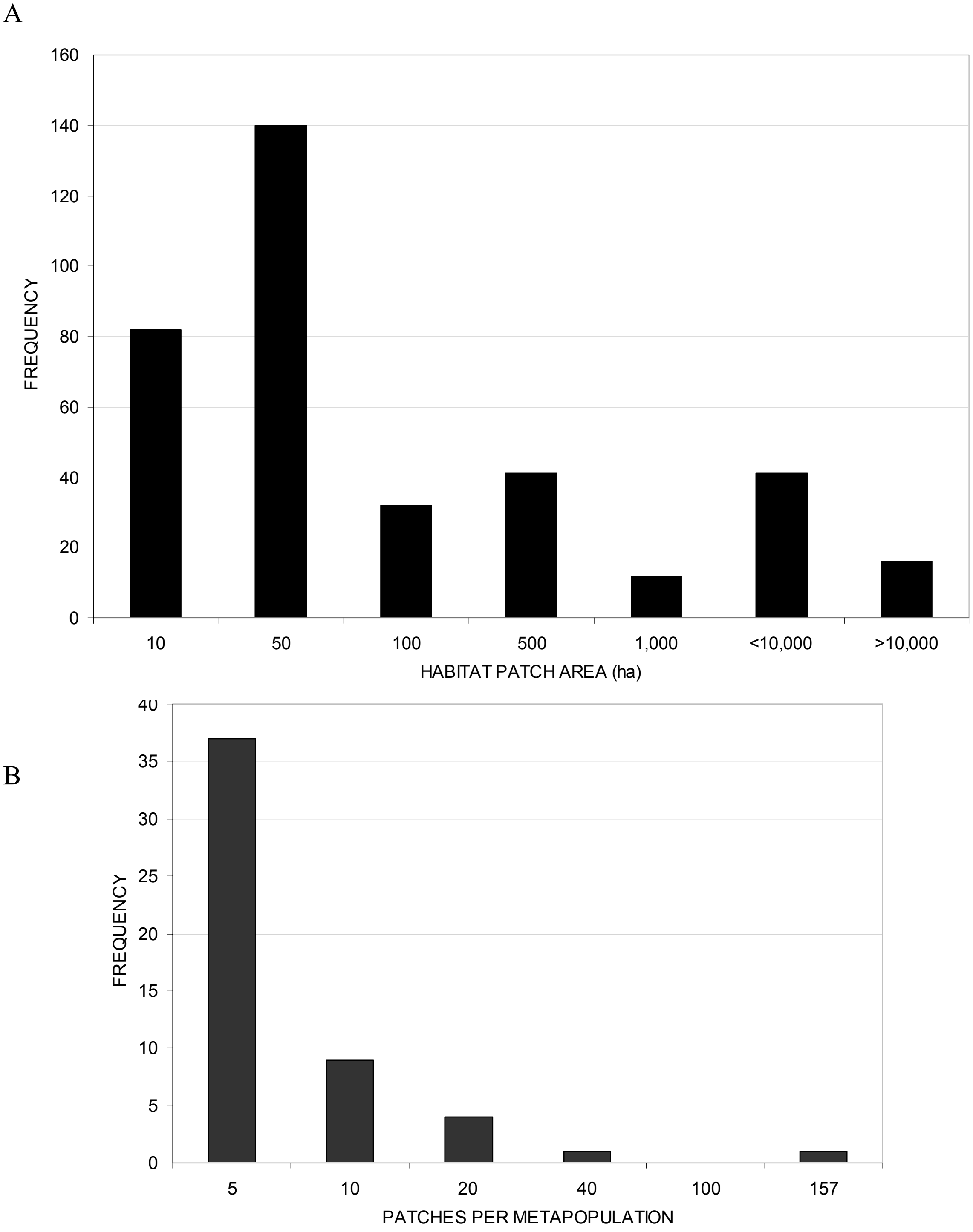


Figure 8.3. A) Frequency distribution of suitable habitat patch sizes and B) patches per metapopulation for Northern Bobwhite in Illinois, as determined from a model of landscape-level habitat suitability.

Table 8.6. Time to extirpation for Northern Bobwhite metapopulations in Illinois regressed against population size (nee habitat area) and number of populations in metapopulation.

Parameter	β	SE	*t*	*P*	Type I Sums of Squares
Intercept	-7.43	0.59	-12.58	<0.0001	
Log(*n*)	11.28	0.27	42.22	<0.0001	5770.2
Neighbors	0.17	0.08	2.19	0.0338	10.2

DISCUSSION

Dispersal

My review of literature published since Leopold's writing of *Game Management* largely agrees with his findings and supports the use of a 2-km buffer around islands of optimal habitat. Conventional wisdom suggests bobwhite, except in rare circumstances, are rather sedentary in their dispersal movements. Leopold (1933), recounting Stoddard's studies of the middle 1920s, suggested three-quarters of bobwhite moved no more than 0.6 km in a year. Only 9% moved as much as 1.6 km, a proportion slightly higher than predicted by the dispersal function. Most of the longer movements reported by Leopold were by solitary individuals; only 1 covey moved as much as 1.6 km. Errington and Hamerstrom (1936) reported even more conservative movement, as only a few coveys out of >11,000 quail moved >1.6 km; if we assume a few coveys is ~45 individuals (4 coveys × 11 birds·covey^{-1}; C. K. Williams, *personal communication*), this translates to ~0.4% moved >1.6 km. Certainly this is enough to maintain panmictic genetic structure, but it is doubtful that this is sufficient movement to maintain metapopulation dynamics, especially if current population extirpations occur at a rate greater than historical frequencies due to anthropogenic causes.

Leopold (1933:74) offered a caveat that throws a potential wrench into any conjecture on dispersal in bobwhite; he wrote, "in quail, there is reason to suspect that annual mobility increases toward the edges of the geographic range." Thus, in Illinois, a 2-km buffer may be too conservative. This points to the need for additional information regarding the dispersal behavior of this species. Clearly, too little information regarding dispersal behavior is known to conjecture with confidence as to whether disjunct populations of bobwhite may function as metapopulations in Illinois.

Landscape Correlates of Colonization and Extirpation

Extirpation.—Both competing models of extinction probability included $\text{MCA2}_{\text{Grass, 5,000 ha}}$ and $\text{IJI}_{\text{Small Grains, 5,000 ha}}$. One model contained $\text{MCAI}_{\text{5,000 ha}}$ and $\text{Human}_{\text{500 ha}}$, whereas the other contained $\text{CLAND}_{\text{Woods, 50 ha}}$. $\text{MCA2}_{\text{Grass, 5,000 ha}}$ is the mean area of disjunct core grassland; I interpret the negative effect of increasing disjunct grassland core size as core size increased, grassland edge became relatively rarer in the landscape. This suggests large grassland patches may be, to a large degree, unusable probably because the core areas of grass patches do not possess sufficient woody cover for bobwhite. As interspersion and juxtaposition of small grain agriculture increased, that is, small grain fields approached equal adjacency with all other land uses, probability of extirpation increased. Thus, bobwhite are more likely to persist in areas where small grain agriculture is distributed in an somewhat aggregated manner. This may be intuitive in 1 instance, and counter-intuitive in another, in that bobwhite presence increases with increasing amounts of small grain in the landscape whereas abundance increases with the availability of small grain edge (Chapter 7). It seems Illinois landscapes with large amounts of small grain agriculture, situated in relatively small fields, in close proximity to each other would offer the best situation for bobwhite.

One final factor associated with bobwhite extirpation was human habitation. The amount of the landscape devoted to human land use (urban and suburban communities) negatively affected bobwhite. The USDA Natural Resources Conservation Service indicated >6.5 million hectares of land were developed in the United States between 1992 and 1997, increasing total land area devoted to human habitation from 4.6% to 5.4%; in Illinois, urbanization increased from 7.8% of the total land surface in 1982 to 9.4% in 1997. Clearly, as urbanization increases, bobwhite are at increased risk of population extirpation.

Colonization.—Colonization was a function of total core area in the landscape across all land use practices, mean core area per woods patch, mean nearest neighbor of row crop agriculture, mean proximity of all land use practices, and amount of woods. As proximity of row crop fields decreased, colonization of suitable habitat was increased. As all land uses became less isolated (with row crops as a notable exception given the previous interpretation), probability of colonization increased. Bobwhite require woody cover and, based on these results, appear to require woody cover for colonization as well. Probability of colonization increased as both the amount of woods in a 50 ha area and the size of forest cores in a 5,000 ha landscape increased. However, as was noted earlier, too much woody cover in the landscape depresses rates of population occupancy and abundance (Chapter 7).

Habitat/Population Structure

Landscape-level habitat optimal for bobwhite appears patchily-distributed in northern and east-central Illinois with much of this habitat appearing as islands within a matrix of varying (but less than optimal) suitability. This patchy distribution does not by itself conform to the requirements of a metapopulation (Hanski 1999). However, local-area and site-level conditions, bobwhite response to dispersal corridors, predator distribution, weather, and other factors may further limit habitat suitable for bobwhite, creating the potential for metapopulation dynamics within this patchy landscape.

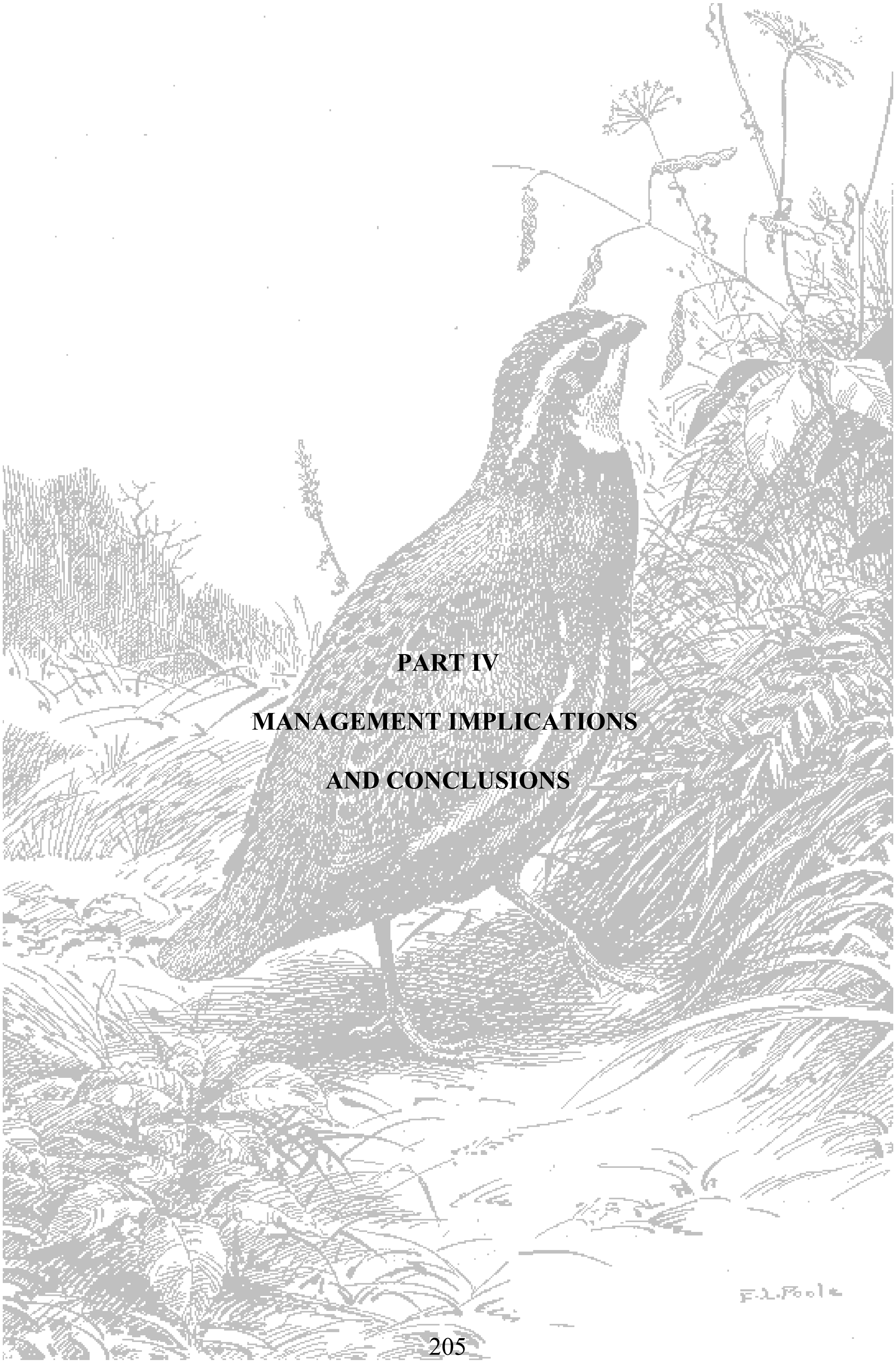
A continuous grouping, or network, of optimal habitat effectively constitutes a metapopulation. Levins (1969) defined a metapopulation as a “population of populations”. For Illinois, the islands of optimal habitat are the populations, with some islands being occupied by bobwhite and others being vacant.

Results of the mechanistic model were, in general, more pessimistic than those for the stochastic Markov Chain implemented earlier (Chapter 5). This is surprising in that a major prediction of metapopulation dynamics is that even in a network of subpopulations characterized by local instability, the metapopulation as a whole may be regionally stable (Hanski and Gilpin 1997, Hanski 1999). Without synchronization of dynamics, some populations are usually stationary or increasing when others are in decline. Ostensibly, these declining populations are rescued from extirpation or the habitat re-occupied by dispersers from these neighboring habitats.

I demonstrated that a degree of synchronous dynamics existed in some regions of Illinois (Chapter 4). This synchrony would have the effect of precluding rescue since all of the populations within a region would exhibit a declining abundance if the population in danger also exhibited a declining abundance.

The model was not, however, parameterized to account for the observed synchrony. Thus, the model probably should have predicted longer times to extinction than did the stochastic Markov Chain. Even though this model has been successfully used for various European galliforms, it may be that this simple mechanistic model was poorly configured for bobwhite. The parameter values implemented in the mechanistic model were in each case optimistic. This was necessary to achieve a realistic growth rate (λ), a growth rate similar to the observed stationary or slightly declining abundance. The parameter values used in the model by themselves were not extreme, but in concert should have evoked a positive growth rate. That they did not suggests that this approach was likely flawed. Furthermore, to obtain positive growth rates would have required seemingly unrealistic parameter values (e.g., mean clutch size >16). Thus, the true benefits of this approach is likely the ranking of population networks rather than any predicted times to extinction. If predicted time to extinction is linearly related to true time to extinction, which seems reasonable, then the model results are useful in prioritizing areas for management consideration. This is developed in greater detail in the next chapter.

These analyses represent tests of an initial hypothesis that large-scale habitat features interact with local-level considerations to influence the distribution and relative abundance of bobwhite. Results indicated the potential usefulness of considering historical effects, spatially-autocorrelated data, and large-scale landscape factors when developing models of animal abundance. The models generated represent spatially-explicit hypotheses as to how bobwhite are associated with their environment. Clearly, the next logical step is to select areas to test the models to evaluate their accuracy and applicability.



PART IV

MANAGEMENT IMPLICATIONS AND CONCLUSIONS

CHAPTER NINE

ECOLOGICAL FEASIBILITY OF RESTORING BOBWHITE TO UNOCCUPIED OR SPARSELY POPULATED AREAS IN ILLINOIS: PRIORITIZING HABITAT FOR MANAGEMENT

It has been suggested by some bird protectionists that the bobwhite should be removed from the game-bird list and be rigidly protected at all seasons as a song bird.
Charles Bent

Projections of population trends, after incorporating stochastic uncertainty (Chapter 5) and population configuration (Chapter 8), indicated most Illinois populations of bobwhite will be extirpated within the next century. Uncertainty as to the exact time of these extirpations is due to uncertainty in the frequency of weather catastrophes (Chapter 6), the rate at which suitable habitat will continue to be converted to unsuitable land use practices (Chapter 2), and variations in the methods used to estimate time to extinction. Regardless, maintaining the status quo will not likely work to resurrect these populations. As was suggested by the apparent spread of bobwhite from their restricted distribution after the severe winters of the late 1970s (Chapter 3), increasing abundance of bobwhite may lead to re-occupation of extirpated habitat if the habitat is within the dispersal distance of the species. For habitat that is isolated, either because habitat is too far removed or barriers to dispersal intervene between nearby habitat, alternatives to natural recolonization must be considered to counter current declines in the state. Translocation of bobwhite to properly-identified habitat offers 1 such alternative (Wolf et al. 1996). My objective in this chapter was to prioritize previously identified quail population networks for management action, with the prioritization focusing on identifying habitat suitable for recolonization.

METHODS

I ranked subpopulations based upon the number of subpopulations within its metapopulation network (NHBR), mean landscape suitability of subpopulations (LHSI), total area encompassed by the subpopulation (AREA), latitude of the subpopulation (NRTH), and the proportion of neighbor subpopulations predicted to be unoccupied or sparsely occupied (UNOC). Predictions as to whether certain habitat was occupied or unoccupied was based on subtracting patch probabilities from the suitability models defined in Chapter 7 (Table 7.1, Appendix 7.C). Values for the remaining criteria were derived from Chapter 8. I assessed various weightings of each criteria to determine the sensitivity of rankings to changing emphasis, but found that rankings varied little. For instance, due to results of Chapter 8 I initially considered weighting AREA considerably more than NHBR but because the results of the various weighting schemes did not change the overall ranking, I abandoned this approach. I concluded with only a simple ranking based upon the sum of equally-weighted ranks across the 5 criteria.

In this chapter, I ranked the landscapes for translocation based on ecological criteria alone. However, choosing a suitable area for population reestablishment should be based not only on the biological characteristics of the species, but also on socio-economic factors such as the attitude of landowners in the area effected (Jungius 1985).

Political and social considerations (e.g., proximity to Chicago hunters) have not been considered in this, but may easily be incorporated to effectively decide future courses of management action.

RESULTS AND DISCUSSION

One-hundred-seventy-one patches (1,944 km^2) were predicted to be either unoccupied or sparsely occupied (Fig. 9.1; Appendix 9). Mean landscape suitability in these patches was 0.517 ± 0.001, below the lowest observed occupied habitat suitability index value (Chapter 7). Twelve entire networks of suitable habitat were predicted to be devoid of functioning bobwhite populations.

The top 2 patches for possibly translocating Northern Bobwhite based on ecological criteria were situated in Tazewell County, and were adjacent to the large contiguous patch of occupied habitat occurring throughout western and southern Illinois ("mainland") (Fig. 9.2). A large number of candidate patches occurred in Mercer County; translocations here and in eastern Stephenson County have the effect of spreading risk of extirpation across a larger area since these populations may have unique population trajectories. Patches of unoccupied habitat closest to Chicago were situated in Kankakee County, and translocations here have the dual benefit of spreading extinction risk and possibly increasing hunting and viewing opportunities for Chicago residents. Each of these top choices appears to be associated with nearby occupied habitat. Thus, the reason for the depauperate state of the patch may either be due to the lack of suitable site-level habitat or the lack of dispersal corridors between occupied and unoccupied habitat. Only field validation of these models will provide sufficient information to distinguish these potential causes.

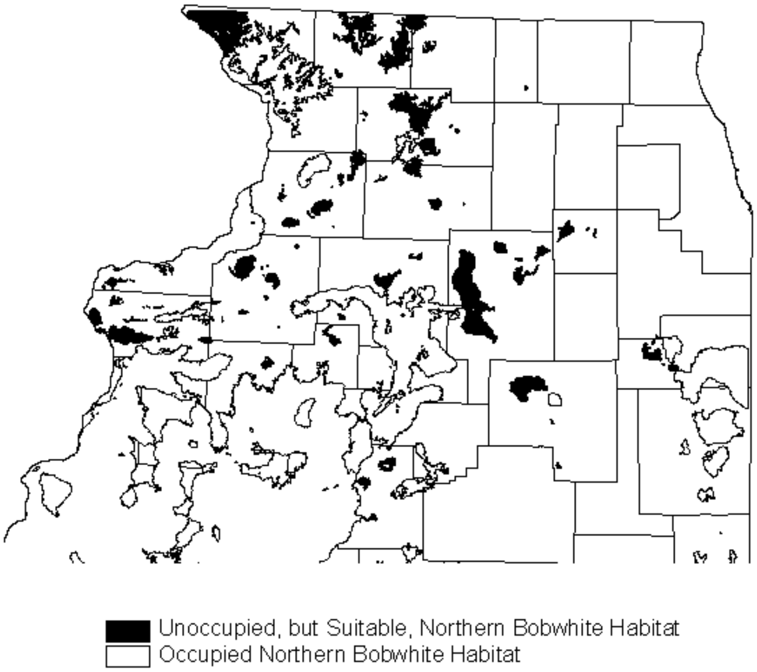


Figure 9.1. Suitable Northern Bobwhite habitat in Illinois predicted to be unoccupied or sparsely populated (in black) based on effects of historical winter weather of the late-1970s.

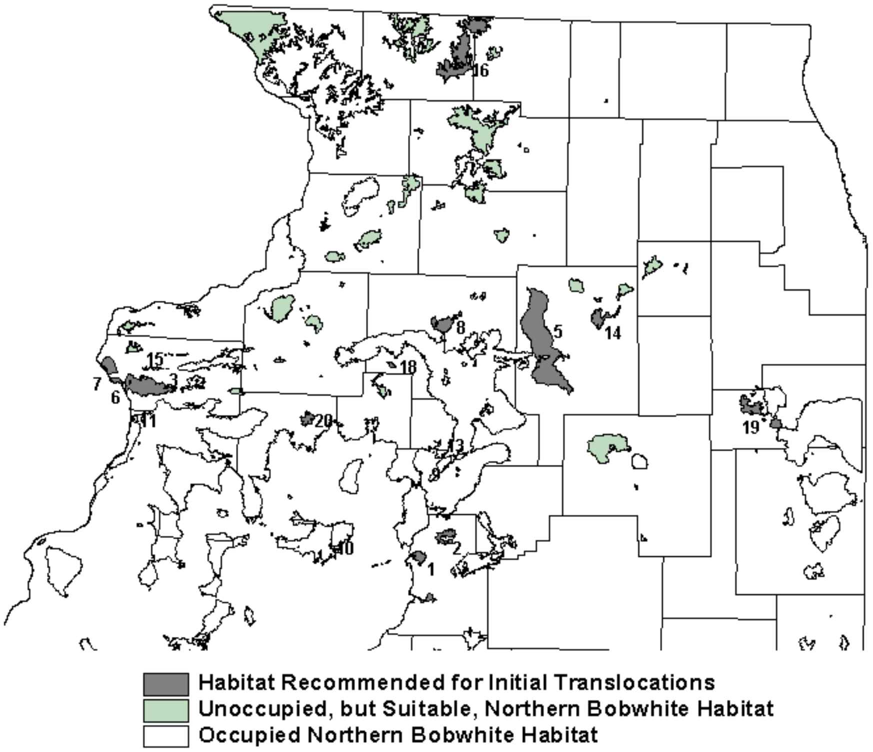


Figure 9.2. Habitat most suitable for translocation of Northern Bobwhite. The top 20 choices are numbered and are a darker gray.

CHAPTER TEN

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

If we know both the historical and current biotic and abiotic factors most important in determining distribution, abundance, and persistence of a species we may be able to predict future impacts and future directions of populations, and thus approach management with a more focused response. My objectives in this dissertation were four-fold, to 1) estimate historical temporal and spatial patterns in bobwhite population dynamics and determine their contribution to current dynamics; 2) estimate bobwhite population distribution and abundance in Illinois; 3) determine the structure of current populations; and, 4) determine environmental and historical factors at multiple spatial scales contributing to their distribution, abundance, and persistence.

Effects of winter weather were apparent in historical and extant patterns in distribution. There was some residual influence of the 1970s winters on extant distribution and abundance with most of the patches predicted to be unoccupied or sparsely occupied located in the northern portion of the state.

My model of bobwhite distribution indicated nearly contiguous habitat throughout the southern and west-central portion of Illinois. This is largely an artifact of the scale at which bobwhite selected landscape characteristics. That the 5,000-ha scale is the most important scale (of those considered) for determining bobwhite distribution and abundance suggests population processes influencing births and deaths are the factors being affected at this scale. Recently, Guthery (2001; Guthery et al. 2000) indicated an area equaling 5,000 ha is likely the minimum size necessary for long-term persistence of bobwhite in the presence of stochastic perturbations to population processes.

Plots of the 2 competing and the averaged ARIMA models created from NABBS data (Chapter 4) were used to forecast abundance (Boyce and Miller 1985) with each model indicating a dampening of abundance to slightly above the current mean condition. Thus, given the phase-forgetting nature of the time-series, I suggest that until the next major perturbation in the system, bobwhite should persist in Illinois if the deterministic trend in abundance can remain positive. Between 1980 and 1999, NABBS data indicated bobwhite abundance declined a non-significant 1.1% · yr^{-1} (based on estimating equations, NABBS estimated a decline of 0.35% · yr^{-1} [$P = 0.64$, $n = 74$]). Thus, efforts to reverse this slight downward trend, if it even currently exists, should aid in insuring future persistence of bobwhite in Illinois. However, unless major steps are taken, the next major perturbation may throw Illinois populations of bobwhite into such a wild oscillatory pattern as to bring about numerous local, if not regional, extinctions.

If local populations are linked by dispersal, metapopulation theory predicts the network of populations may be viable even if none of the local populations are viable. Thus, even though extirpation was predicted for several areas within the historical quail range, populations in these areas may be sustained by dispersal from neighboring areas (Chapter 8). I found most bobwhite habitat in Illinois was situated as mainland-island type metapopulations (Chapter 7). The contiguous habitat of the southern and west-central portion of Illinois likely acts as a source of immigrants for the outlying island habitats. Within this mainland habitat, current population trajectories have identified some areas in need of closer scrutiny. Increased monitoring of bobwhite population dynamics and their habitat is warranted in counties extending in a line from Hardin to Madison Counties and from Clinton to Lawrence Counties. Bobwhite in these counties within the historical quail range are predicted to be at imminent risk of extirpation (Chapter 5). Relatively large local populations in these counties will gain most by improving local and landscape conditions necessary for long-term persistence.

CLIMATE

Given that environmental perturbations are apparently an important organizing force in bobwhite population dynamics in Illinois (Chapter 6; Thogmartin et al. 2002), good estimates of future bobwhite persistence hinge on identifying future frequency and patterns of major climatic events. This endeavor, however, is problematic in that it is confounded by global warming and the unknown consequences this may have to regional weather phenomena.

Identifying effects of future weather and anthropogenic alterations to the Illinois landscape on bobwhite population dynamics will assist in determining whether predictions of bobwhite population persistence are correct. Climate variability, rather than mean climate conditions, will likely determine whether bobwhite in northern Illinois can persist for any meaningful length of time. If extremes in severe winter weather increase, bobwhite occupying disjunct habitat (Chapter 7) will likely be extirpated without hope of rescue from surrounding occupied areas. While future mean climatological conditions are fairly well understood (Houghton et al. 1996), relatively little is known regarding future patterns in climate variability (Easterling et al. 2000, Meehl et al. 2000). Predicted increases in mean temperature should lead to decreases in the number of cold days and increases in overnight lows (Easterling et al. 2000, Meehl et al. 2000), if variability remains consistent with current conditions. Fewer cold days may reduce the number of days where snow presents an impediment to movement for bobwhite, leading to increased winter survival. This increase in minimum temperatures will occur only if variability around the rising mean is similar to current conditions. Several studies suggest this may be the case (Meehl et al. 2000).

A possible confounding factor is that increases in greenhouse gases, which are responsible for global warming, are predicted to increase intensity of precipitation (Giorgi et al. 1998, Meehl et al. 2000). Giorgi et al. (1998) projected increases in extreme precipitation events (or the lack thereof) over the central plains of the US. For instance, the probability of drought during midsummer should increase in the midcontinental US. The increase in precipitation with temperature will likely not be in the form of snow, as extent of snow cover varies inversely with temperature (Easterling et al. 2000).

Caveats regarding climate variability aside, increasing mean temperatures should initially promote favorable conditions for occupation of northerly habitats by reducing winter severity (Roseberry 1989, Thomas and Lennon 1999, Parmesan et al. 2000). Reduced overnight cooling will allow bobwhite to maintain higher nighttime metabolic rates for a longer period of time, reducing the probability of individual mortality and population extirpation. Visser et al. (1998), however, found warmer springs in the Netherlands led to mistimed reproduction in Great Tits (*Parus major*), whereas Moss et al. (2001) suggested Capercaillie breeding success in England in response to earlier spring was lowered due to either a reduced plane of nutrition in laying hens or chicks hatching after the peak in larval insect abundance. Roseberry (1989) suggested changes in land use and agricultural practices as a response to changing mean temperatures may have a greater long-term effect on bobwhite. Thus, a simple increase in mean temperature has unknown consequences to bobwhite persistence.

Uncertainty regarding the phenology of and extremes in precipitation and temperature, especially their timing (or season) and interaction, make it difficult to predict future impacts of climate change on bobwhite populations in Illinois. Projections (Chapters 5, 9) suggest the Illinois landscape, as it is currently configured, will likely sustain abundant populations of bobwhite in the historical quail range, but populations in the disjunct habitat of northern and east-central Illinois will likely face severe constraints on continued persistence despite apparently favorable changes in winter conditions.

MODELS

A model is a physical or abstract representation of the structure and function of a real system. Statistical models cannot be true (Anderson and Burnham 2001); they can, however, be useful. The importance of a model is determined by its reliability in prediction or decision-making (Mitro 2001). Thus, a good statistical model should be more reliable than a faulty one.

Levins (1966) suggested a good model must be comprised of 3 features: generality, realism, and accuracy. The generality of the bobwhite habitat models that I developed will be determined by their application to landscapes in other states or at other times. Because habitat models developed by other authors contained similarities to those developed for Illinois, they suggest a certain degree of generality. With the availability of NABBS data sets for other states and the digital National Land Use/Land Cover (US Geological Survey, Sioux Falls, South Dakota, USA), these models could be extended nationwide to test their degree of applicability. The degree to which these models are realistic, however, is a concern. There will undoubtedly be discrepancies when applied in different areas; for instance, number of days of winter snow cover may not be important when applied over a wider area such as the southeastern US. , but given their apparent generality and the purported relationships between landscape characteristics and bobwhite, the models appear generally realistic within the context for which they were developed.

Regarding accuracy, the logistic model was highly accurate for areas where bobwhite were common; it did a poorer job of defining suitable habitat outside of these areas. Poor model performance in these areas is likely due to the existence of remnant populations within areas of suitable site-level conditions. These areas likely act as population sinks because of their generally small size (Pulliam 1988, Pulliam and Danielson 1991). Populations occupying sink habitats exhibit greater temporal variability than do source populations (Beshkarev et al. 1994), placing them at risk of chance extirpation. Identification of source populations and habitat, if they exist, is critical for sustaining populations, because regional existence of many species is dependent on successful reproduction from population sources (Pulliam 1988, Pulliam and Danielson 1991). However, it is unlikely that landscape conditions can be improved to a sufficient degree as to ensure that these suitable sites remain occupied.

Influence of Scale

Ribic and Sample (2001) found Grasshopper Sparrows (*Ammodramus savannarum*) and Eastern Meadowlarks (*Sturnella magna*) were most associated with landscape factors at a 20 ha scale, whereas Savannah Sparrows (*Passerculus sandwichensis*) and Bobolinks (*Dolichonyx oryzivorus*) were most associated at a 233 ha scale; they did not assess influences of the landscape at larger scales than 233 ha so it is unclear whether these migratory grassland songbirds may be influenced at even larger scales like the bobwhite. For instance, McCoy (1996) found grassland birds were influenced at scales between 300 and 8,000 ha.

As the scale of analysis changes the effect on the species of interest changes as well. Johnson (1980) described 4 orders of selection. The first order of selection is the distribution of a species across a geographic range, as determined by environmental influences on population births, deaths, and movements. The second order of selection concerns the placement of individual home ranges within this range. Because results of the models I developed indicated important influences at the 5,000-ha scale, my results provide more appropriate inference about the bobwhite's selection at the first order of selection.

Influence of Population Size

The mechanistic model of bobwhite metapopulation dynamics demonstrated that the most effective means to stabilize bobwhite populations in Illinois was to increase the gross amount of suitable landscape habitat. Increasing the amount of suitable landscape habitat has the effect of raising potential population size, which in turn reduces effects of both demographic and environmental stochasticity (Guthery et al. 2000). Increasing the size of suitable habitat also has a small effect on reducing distances between neighboring landscape patches, promoting successful dispersal. However, managing for successful dispersal is not the most effective means by which to stabilize populations; the effect of neighboring habitat on time to extinction was simply too small to play much of a role in bobwhite metapopulation dynamics. Thus, the question becomes, how might management increase the area of suitable landscapes. Models of bobwhite presence and abundance clearly suggest small grain agriculture has the greatest chance at increasing landscape suitability in today's agro-environment, suggesting state agricultural policies should promote small grain cultivation. Increasing small grain cultivation at the expense of row crop cultivation would have the consequence of increasing landscape evenness (increasing Shannon's J') and valuable edge habitat.

MANAGEMENT STRATEGIES

More than half of all land in Iowa, Illinois, and Indiana is cropland (Best et al.

2001). It is within this agricultural context that wildlife habitat must be created and maintained. That the vast majority of this agricultural land is privately held increases the difficulty of the task.

The conventional strategy for conserving wildlife on agricultural lands is to reduce the intensity of farm activities and to compensate farmers for their production losses (Muster et al. 2001). However, the current state-wide approach whereby biologists provide technical advice to and enroll landowners in cost-share programs (e.g., Conservation Reserve Program) for habitat improvement produces only isolated pockets of favorable habitat amongst areas of poorer habitat (Weber 2000). This approach dilutes effects of habitat improvement on upland wildlife, including bobwhite. A more efficacious approach for management would be to focus on either areas demonstrating immediate need of management or those areas where bobwhite are predicted to persist for many more generations. Emphasis on the former would be to reverse observed declines in abundance, whereas emphasis on the latter would be in preventing deterioration of strong populations. I have identified areas of Illinois where bobwhite are in clear need of immediate management action (Chapter 5). I have also identified areas where bobwhite appear to be safe over the long term. Aggressively managing the former and protecting the latter will delay, and possibly negate, future population extirpations.

Warner and Brady (1996) provided an excellent review of the necessary characteristics of successful wildlife programs in agricultural environs. One example that combines their suggestions to achieve both population stability and recovery is CURE, North Carolina’s Cooperative Upland Restoration and Enhancement program. Within landscapes of high-quality quail habitat, biologists enroll groups of landowners which together contribute >2,000 ha of contiguous habitat; enrollments are for ≥5 years and are supplemented with cost-share programs such as the Conservation Reserve Enhancement Program or the Wildlife Habitat Improvement Program. State outreach biologists and human dimensions specialists work with landowners within these focal areas to develop management plans enhancing site-level conditions for bobwhite such as promotion of weedy field borders, elimination of fescue, and establishment of native, warm-season grasses. Since bobwhite respond to landscape-scale habitat, managing site-level habitat within suitable focal landscapes will increase the likelihood of persistence in these large areas.

The hope is that nearby landowners will join the program and focal areas will grow well beyond the initial 2,000 ha blocks of managed habitat. The expectation is that 2–10% of habitat can be affected initially, a small amount, but an amount of habitat offering a better chance for success since bobwhite respond to habitat at the landscape-level (Chapter 7). Ideally, 5,000-ha blocks would be the appropriate management unit (Guthery et al. 2000, Guthery 2001).

Wildlife management will likely have to go beyond traditional means to secure wildlife habitat and promote wildlife population persistence. In the Netherlands, for instance, new methods are being tested to compensate dairy farmers for the number of grassland birds produced on their dairylands (Musters et al. 2001); breeding success by 2 threatened species increased >30% on lands operated by compensated farmers, and the costs of this increased reproductive success was less than costs associated with compensation for production losses due to government-imposed habitat restrictions.

Another approach would be to have state agriculture personnel work with landowners to foster production of early-successional products (Gobster 2001) in focal landscapes. Emery (1998, cited in Gobster [2001:476]) reported 138 products from 80 early-successional plant species played important roles in the livelihoods of Michigan households. Thus, a market for alternative agricultural products does exist in the Midwest. Plants offering both a benefit to upland wildlife and humans include wild edible berries such as blueberry (*Vaccinium angustifolium*) and blackberry (*Rubus allegheniensis*, *R. alumnus*) and wild rose hips and petals (*Rosa* spp.). Promoting these non-traditional agricultural products may help to reduce the need for economic incentives for participation by farmers.

TRANSLOCATION

In addition to employing alternative management practices for safeguarding extant populations, increasing the number of viable populations through translocation (Nielsen and Brown 1988) may aid the long-term prosperity of quail in Illinois (Griffith et al. 1989, Wolf et al. 1996). Translocation of bobwhite can be a high-profile public relations tool for the Illinois Department of Natural Resources, promoting support for broader wildlife management efforts in Illinois (Durrell and Mallinson 1987). There are few published guidelines, however, for successful translocation of Northern Bobwhite aside from those of Masked Bobwhite (*C. v. ridgwayi*) (Ellis et al. 1977, Smith 1987). Some insight may be gained through introductions of Gray Partridge (Church et al.

1983), Ruffed Grouse (*Bonasa umbellus*; Lewis et al. 1968, Hunyadi 1984), Ring-necked Pheasant (Wilson et al. 1992), Sharp-tailed Grouse (*Tympanuchus phasianellus*; Rodgers 1992), and Wild Turkeys (Sanderson and Schultz 1973).

Wolf et al. (1996) indicated multiple translocations of wild birds to a suitable focal area may be necessary to establish a regional population; they also found translocation success was increased by the number of birds translocated. If 50 reproductive females in June are the management objective for a particular patch, >150 females may need to be released in February to affect such a result (Wilson et al. 1992). After release, translocated populations should be protected from harvest and should be monitored to gauge release success (Beudels 1980).

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APPENDICES

Appendix 1. Magnitude of research across various scales and levels of organization (sensu Morrison et al. [1998:241]).

Aspect of Scale	Dominant Magnitude
Geographic Extent	Broad-scale: Illinois, 146,000 km^2 (342 km × 621 km); Quail Range, 89,000 km^2 (279 km × 491 km)
Map Scale	Broad-scale: ≥1:1,000,000
Spatial Resolution	Fine-grained: 28.5 m × 28.5 m; Coarse-grained: 500 m × 500 m
Time Period	Mid-scale: Illinois, 1967–1998, 32 yrs; Quail Range, 1975–1998, 23 yrs
Administrative Hierarchy	Mid-scale: Individual Agency (Illinois Department of Natural Resources)
Level of Biological Organization	Mid-scale: Individual Species

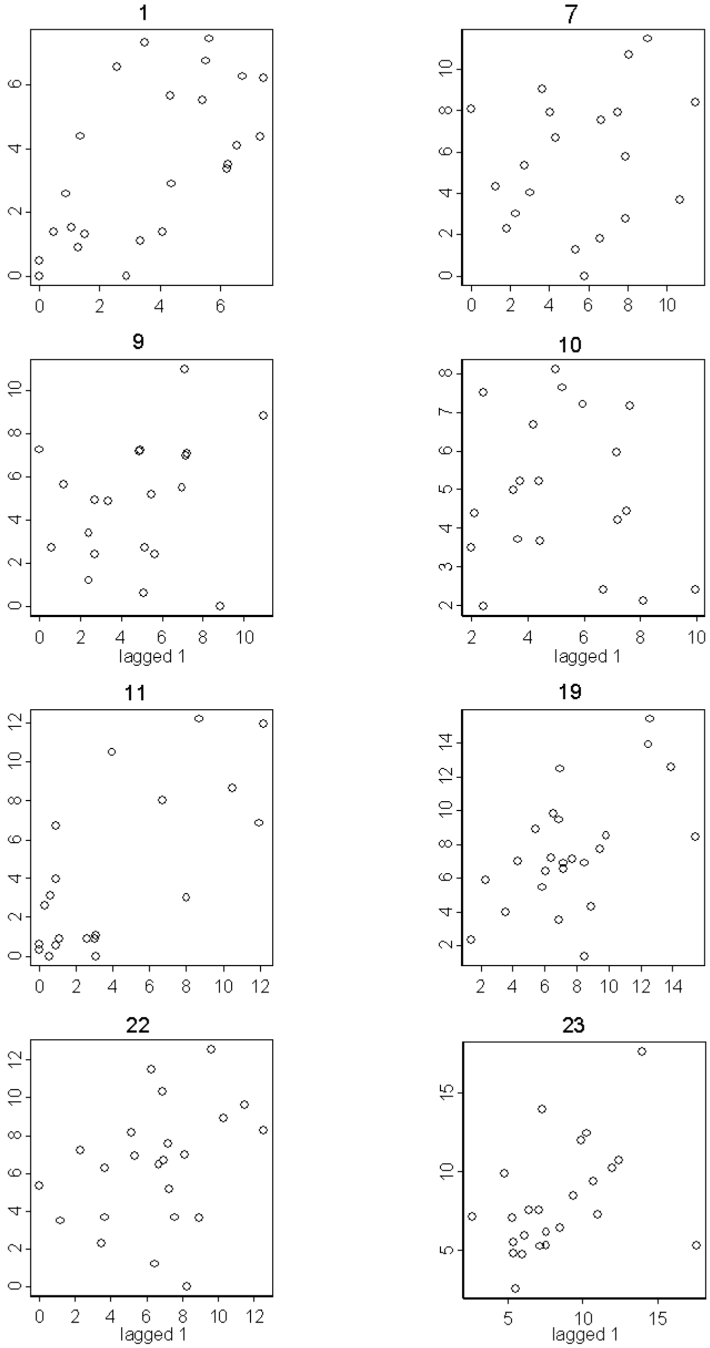
Appendix 2. Northern Bobwhite population trends in Illinois as estimated by estimating equations by the North American Breeding Bird Survey. Slope (β) is the annual percent change in abundance per year, P is the probability value for the test statistic, n is the number of years from which the trend is estimated, s^2 is the variance in route abundance, and $\bar{x}$ is mean count of bobwhite on individual routes for the period 1966–1998.

Route	β	P	n	s^2	$\bar{x}$
1	-4.19	0.194	22	3.23	11.41
2	-7.06	0.039	33	3.42	1.88
3	-14.44	0.099	25	8.75	0.60
7	5.21	0.101	23	3.18	26.22
8	-0.85	0.514	28	1.30	25.61
9	-0.92	0.441	30	1.20	22.90
10	-5.36	<0.001	33	0.99	31.70
11	-11.66	0.286	21	10.93	15.67
13	-18.43	0.004	26	6.47	3.12
15	-6.60	0.185	31	4.98	0.58
16	-11.63	0.002	29	3.80	3.31
17	-1.16	0.798	31	4.54	2.48
18	-11.27	0.138	25	7.59	0.92
19	-0.89	0.607	26	1.73	28.69
20	-0.06	0.949	26	0.90	39.00
21	-8.94	0.003	26	3.03	29.69
22	4.89	0.367	30	5.42	25.50
23	-2.62	0.036	28	1.25	30.68
24	2.21	0.260	32	1.96	29.34
25	-7.84	0.002	26	2.54	25.04
26	-1.11	0.613	27	2.20	28.44
27	-11.95	0.085	24	6.94	10.00
28	-8.77	<0.001	30	1.21	18.37
29	-18.09	0.001	27	5.52	1.44
30	-4.45	0.553	24	7.50	0.83
31	-2.33	0.781	22	8.34	1.05
32	0.33	0.951	21	5.33	1.29
33	-1.37	0.832	25	6.43	15.40
34	-9.18	0.001	31	2.66	3.35
35	-2.53	0.015	26	1.04	42.04
36	-1.12	0.701	29	2.90	24.07
37	-1.62	0.027	30	0.73	46.07
38	-3.19	<0.001	30	0.83	45.63
39	-3.08	0.001	35	0.90	37.69

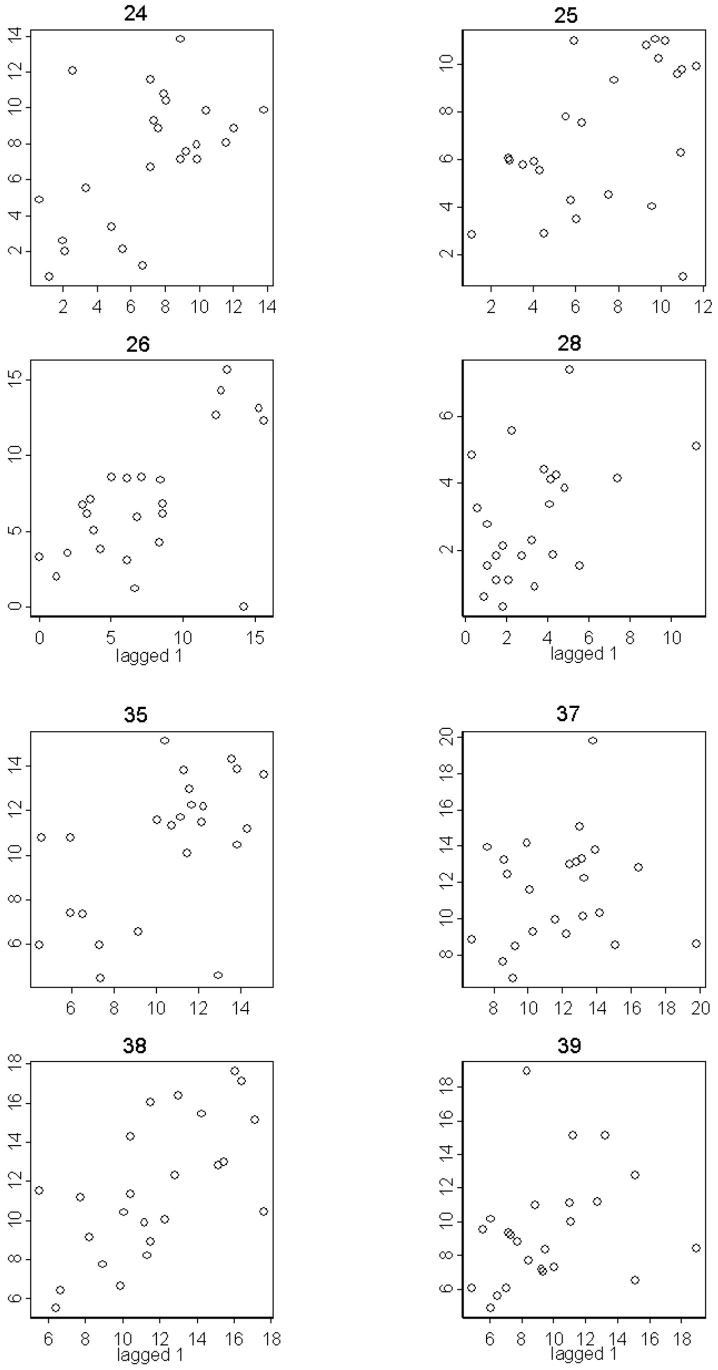
Appendix 2. Continued.

Route	β	*P*	*n*	s^2	$\bar{x}$
40	0.70	0.498	33	1.04	40.09
41	-17.74	<0.001	21	3.53	28.38
42	6.55	0.062	24	3.51	5.88
43	-0.31	0.897	27	2.38	13.74
44	-0.46	0.860	26	2.61	2.38
45	-12.15	<0.001	29	1.87	11.90
46	-4.30	0.009	31	1.65	28.13
47	-24.71	<0.001	30	3.35	3.73
48	-4.58	0.039	31	2.21	33.42
49	-0.42	0.856	24	2.33	40.79
50	-0.22	0.786	32	0.80	36.62
51	-7.76	<0.001	28	1.16	77.32
52	-7.95	0.008	23	3.00	37.52
53	3.98	0.351	24	4.27	21.50
54	0.00	0.995	23	0.72	35.61
55	3.26	0.091	26	1.93	36.19
56	-0.74	0.572	24	1.31	31.13
57	6.07	<0.001	19	1.57	45.00
58	5.00	0.029	21	2.29	39.52
59	-3.81	<0.001	31	0.61	27.26
60	-1.05	0.169	31	0.77	41.13
61	-1.91	<0.001	31	0.45	42.87
62	1.09	0.736	29	3.23	39.34
63	-2.83	<0.001	30	0.44	47.63
64	-2.99	0.091	26	1.77	22.42

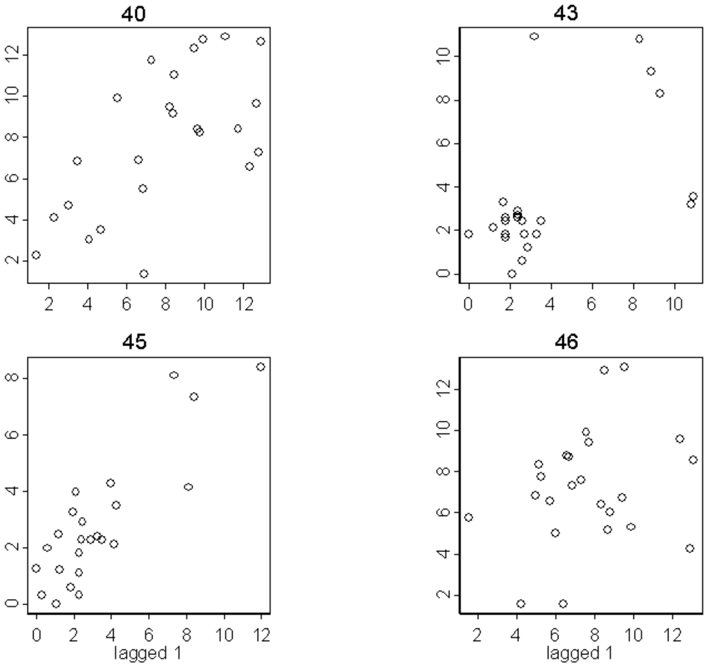
Appendix 4.A. First-order lag plots for each route of the North American Breeding Bird Survey in Illinois meeting criteria for analyses. Ordinate axis is the transformed count data lagged 1 year, whereas abscissa axis is original transformed data.

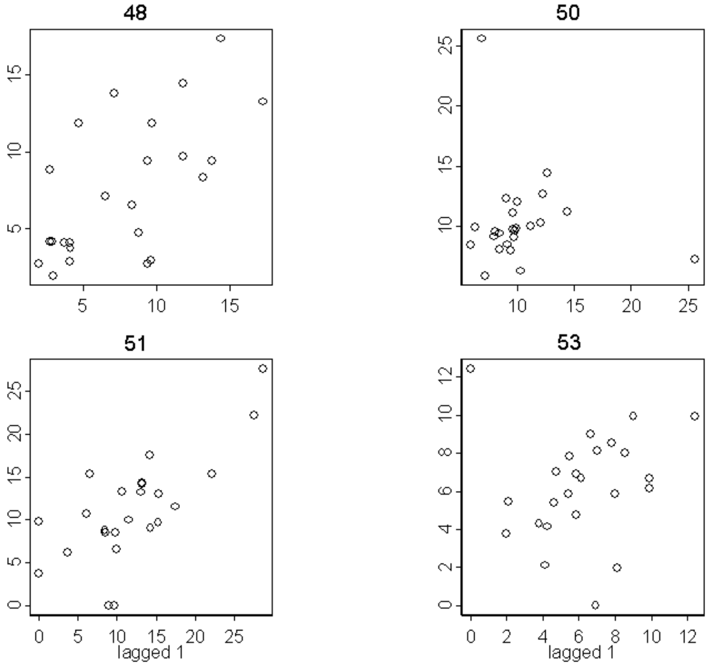


Appendix 4.A. Continued.

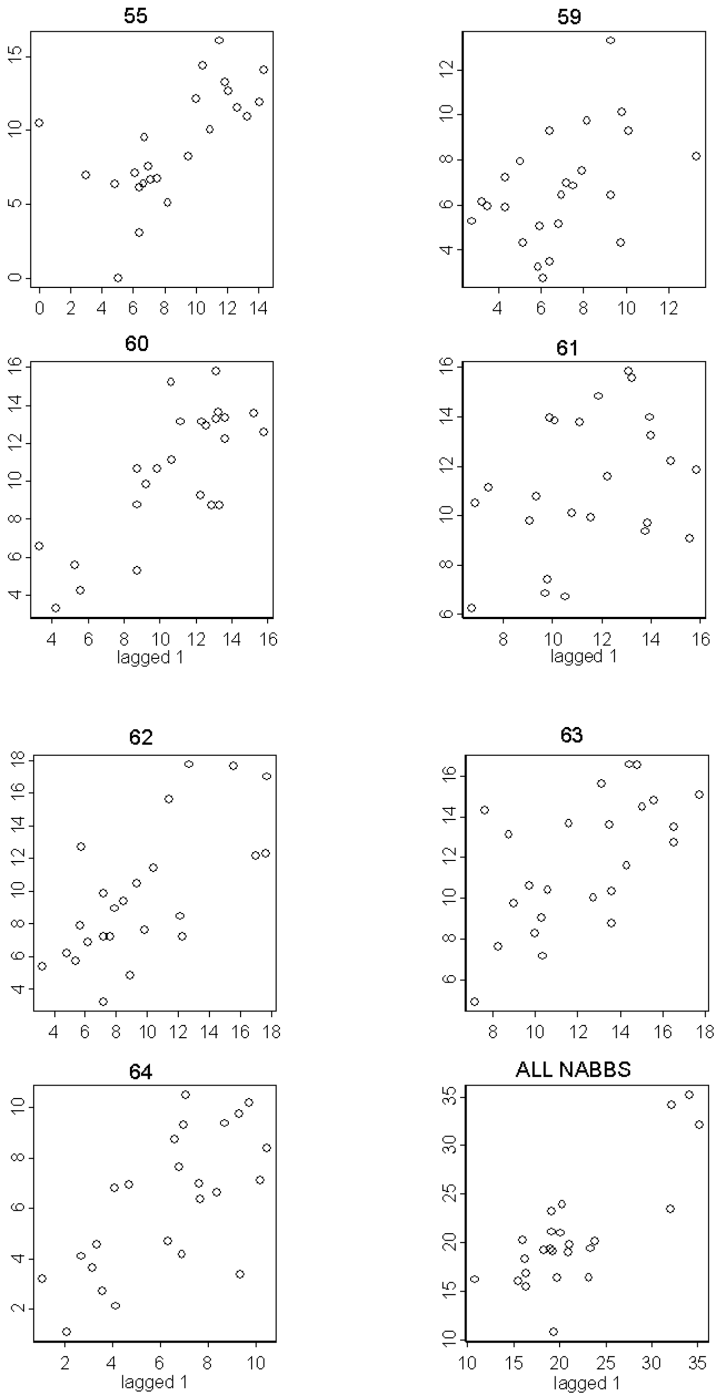


Appendix 4.A. Continued.

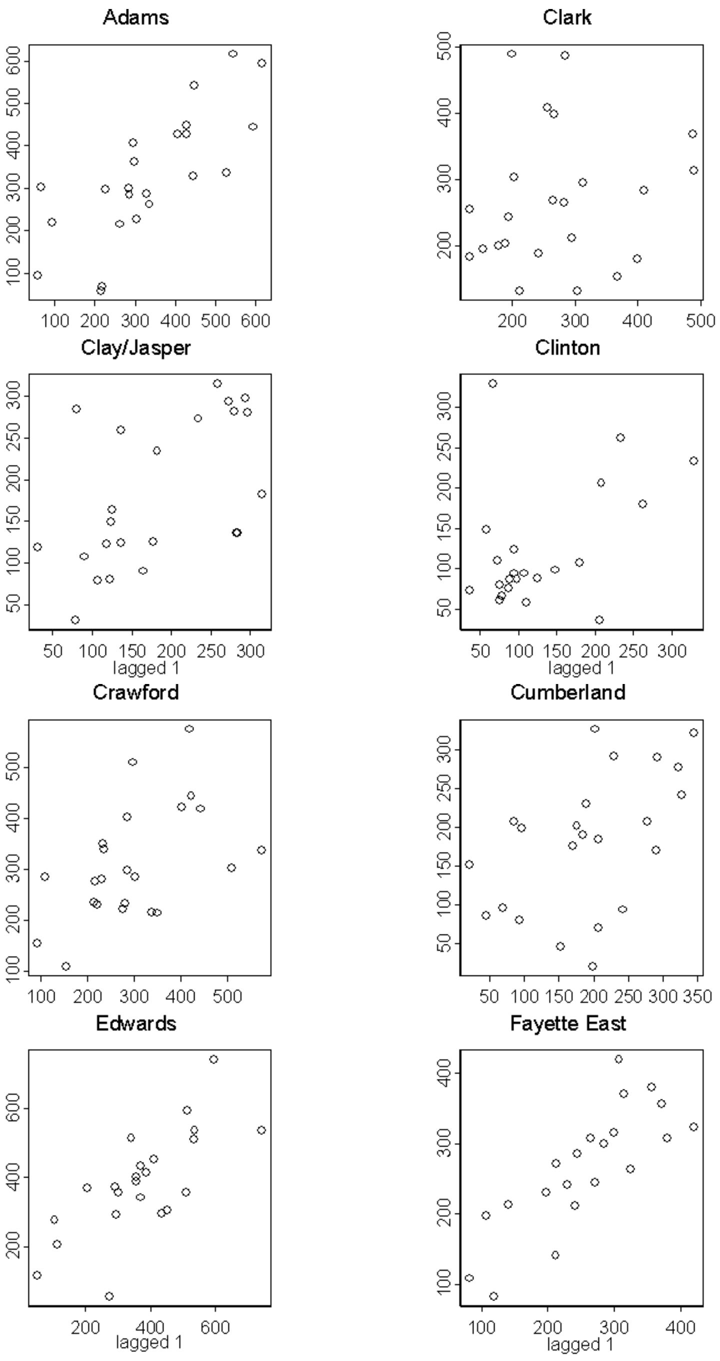




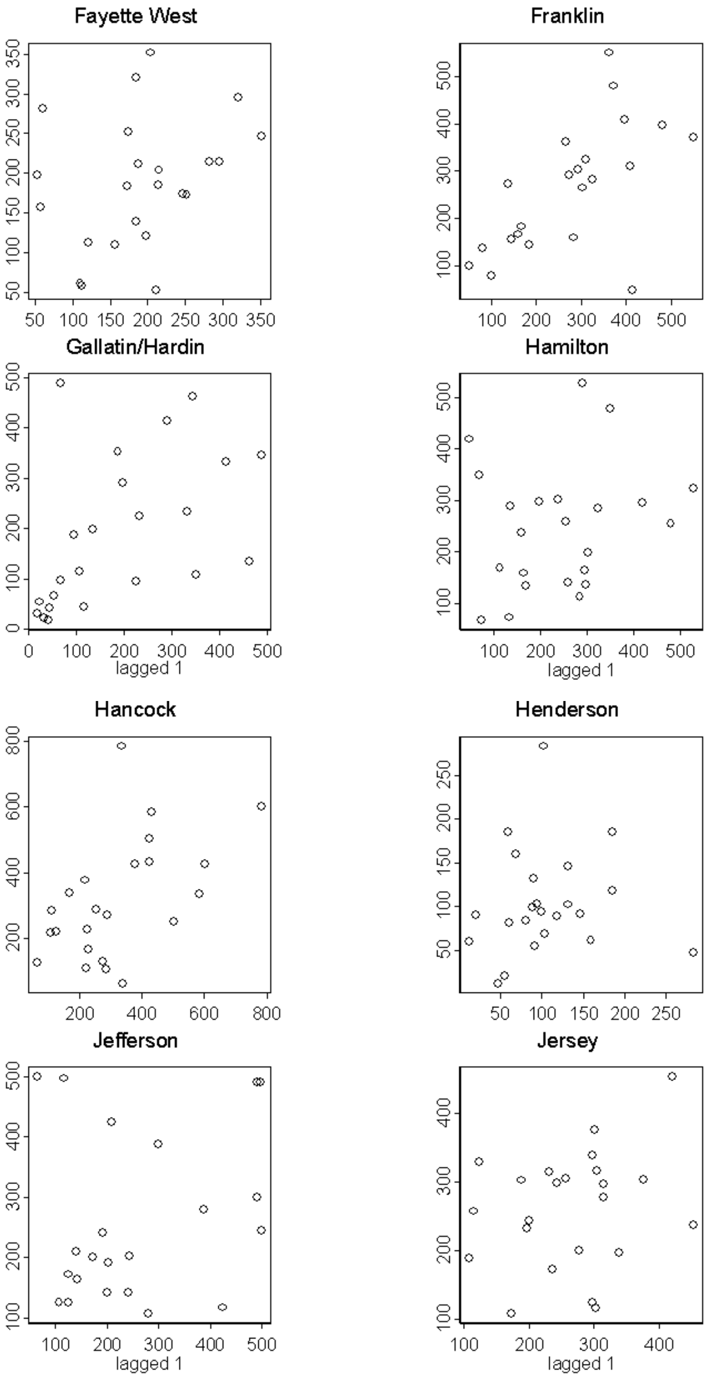
Appendix 4.A. Continued.



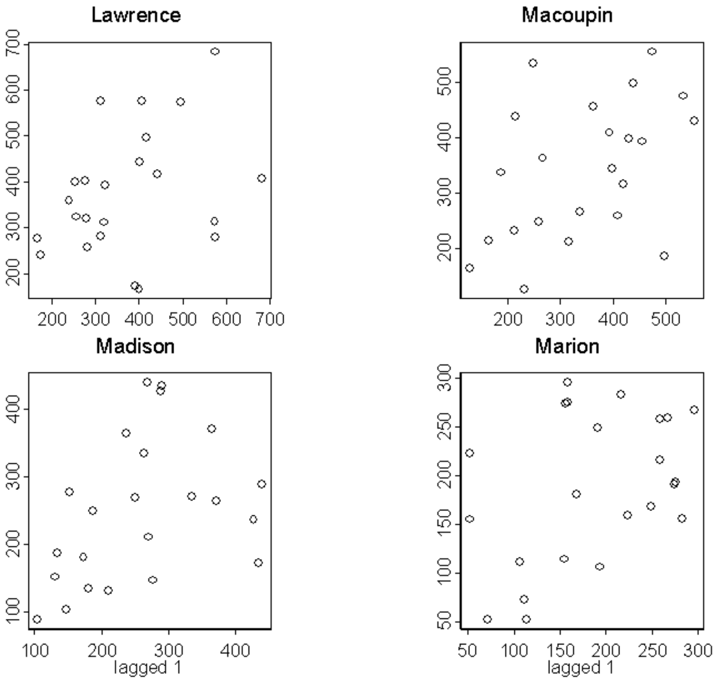
Appendix 4.B. First-order lag plots for each route of the Illinois Department of Natural Resources Bobwhite Call Count Survey meeting criteria for analyses. Ordinate axis is the transformed count data lagged 1 year, whereas abscissa axis is original transformed data.

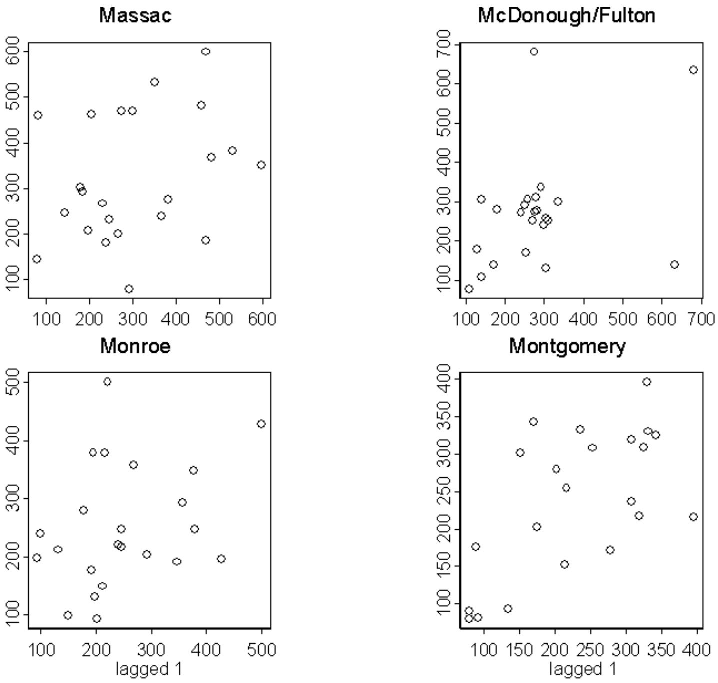


Appendix 4.B. Continued.

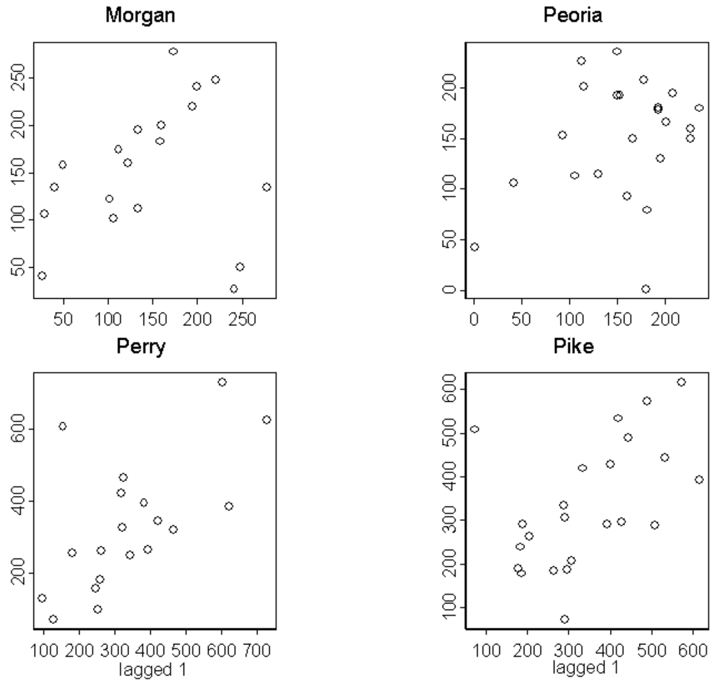


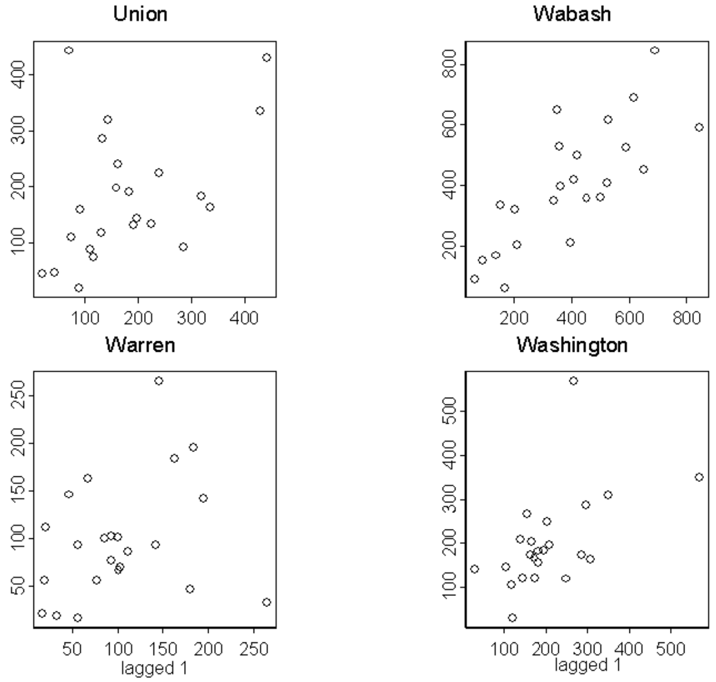
Appendix 4.B. Continued.



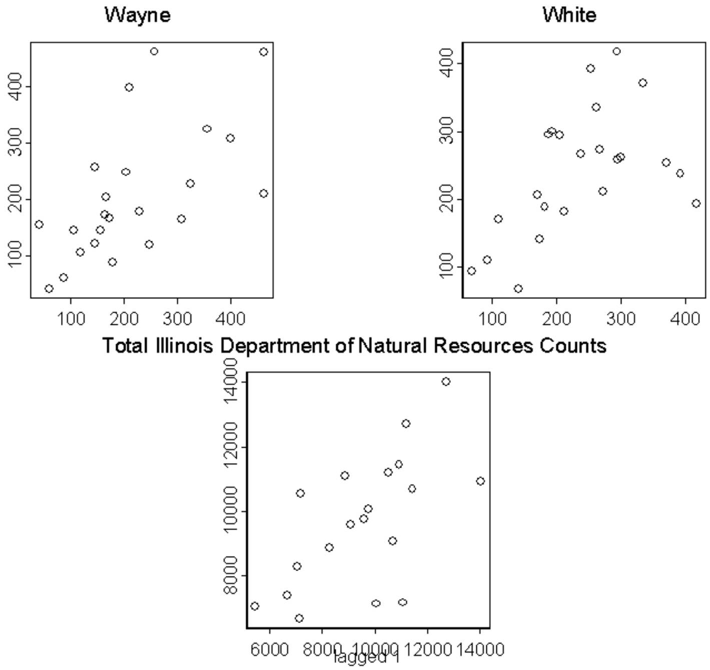


Appendix 4.B. Continued.





Appendix 4.B. Continued.



Appendix 5.A. Route-specific estimates for the rate of change (r_{d0}), serial correlation (ρ), variance in population rate of change (V_r, V_{re}), years to quasi-extinction (T_{qe}), and probability of persistence for the next 100 years for North American Breeding Bird Survey routes in Illinois. *n* is the number of years from which estimates were derived, ρ is the Spearman rank correlation coefficient for consecutive annual estimates of *r*, and V_r and V_{re} are variance estimates for *r* (Foley 1994, 1997). Significant correlations denoted by asterisk.

Route	Name	*n*	r_{d0}	ρ	V_r	V_{re}	T_{qe}	P_{100}
1	Guilford	18	-0.055	0.023	0.818	0.857	18	0.003
2	Mill Creek	18	0	-0.378	0.397	0.179	0	0
3	Holcomb	18	0	-0.500*	0.991	0.330	37	0.068
7	Atkinson	14	0.121	-0.560*	2.352	0.663	19	0.006
8	Geneseo	18	-0.028	-0.369	0.210	0.097	115	0.418
9	Putnam	18	-0.061	-0.204	1.081	0.715	18	0.004
10	Sheffield	18	0.028	-0.319	0.365	0.188	65	0.216
11	Buda	16	0.337	-0.158	0.998	0.726	10	0.000
13	Streator	14	0	-0.311	0.449	0.236	32	0.045
15	Essex	18	0	-0.681*	0.307	0.058	0	0
16	Newark	16	-0.057	-0.404	0.240	0.102	50	0.134
17	Sherburnville	16	-0.018	-0.743*	0.627	0.093	145	0.502
18	New Lenox	12	0.058	-0.686*	0.127	0.024	0	0
19	Gulf Port	18	0.051	-0.154	0.219	0.161	81	0.293
20	Stillwell	18	0.052	-0.400	0.185	0.079	200	0.607
21	Chandlerville	13	0.105	-0.246	0.498	0.301	17	0.003
22	Terre Haute	18	0.053	-0.334	1.537	0.767	18	0.004
23	Williamsfield	18	0.033	-0.336	0.143	0.071	220	0.635
24	Cameron	18	0.121	-0.213	0.504	0.327	23	0.013
25	Bartonville	18	0.082	-0.361	0.285	0.134	102	0.376
26	Monica	18	0.172	-0.391	0.754	0.330	42	0.090
27	Deer Creek	16	-0.032	-0.274	0.473	0.270	38	0.073
28	Mackinaw	18	0.039	-0.426	0.756	0.304	25	0.018
29	Minonk	16	0	-0.829*	0.450	0.042	181	0.575
30	Monticello	16	0	-0.213	0.353	0.229	0	0
31	Fairbury	16	-0.018	-0.806*	0.999	0.107	86	0.311
32	Pontiac	18	0.039	-0.510*	0.870	0.283	27	0.024
33	Dailey	12	0	-0.408	2.652	1.114	7	<0.001
34	Milford	16	0	-0.605*	0.897	0.221	0	0
35	Melrose	18	0.032	-0.289	0.128	0.071	226	0.643
36	Bluff Springs	13	-0.109	-0.148	0.647	0.480	29	0.032
37	Athensville	18	0.007	-0.438	0.223	0.087	182	0.577
38	Concord	12	-0.031	-0.417	0.131	0.054	279	0.699
39	Belleview	18	0.039	-0.333	0.206	0.103	155	0.523
40	Pawnee	18	0.096	-0.294	0.157	0.086	149	0.510

Appendix 5.A. Continued.

Route	Name	n	r_{d0}	ρ	V_r	V_{re}	T_{qe}	P_{100}
41	Clarksdale	14	0.006	-0.231	0.396	0.247	50	0.134
42	Rosamond	18	0.039	-0.524*	0.507	0.158	81	0.289
43	Humphrey	18	-0.089	-0.558*	0.676	0.192	67	0.223
44	Fairland	18	0	-0.572*	0.695	0.189	59	0.182
45	Janesville	18	-0.112	-0.210	0.650	0.425	34	0.053
46	Bradbury	18	0	-0.265	0.298	0.173	88	0.322
47	Humboldt	18	-0.089	-0.615*	0.977	0.233	0	0
48	Martinsville	18	-0.027	-0.340	0.413	0.203	77	0.271
49	Columbia	10	0.435	-0.384	1.565	0.697	23	0.012
50	Mascoutah	18	0.018	-0.397	0.051	0.022	721	0.871
51	Jamestown	12	-0.003	-0.387	2.506	1.108	14	0.001
52	St. Morgan	14	-0.039	-0.287	1.610	0.892	17	0.003
53	Beaucoup	16	0.085	-0.507*	1.874	0.613	23	0.013
54	Burnt Prairie	16	-0.036	0.052	0.051	0.057	276	0.696
55	Mount	14	0.392	0.003	0.982	0.987	16	0.002
56	Olney	14	-0.210	-0.041	0.851	0.783	20	0.007
57	Flora	11	-0.270	-0.258	1.396	0.823	19	0.005
58	Birds	14	0.013	-0.625*	2.372	0.548	29	0.031
59	Pulaski	18	0.012	-0.613*	0.179	0.043	361	0.758
60	Bremen	17	-0.031	-0.286	0.083	0.046	348	0.750
61	Belknap	18	-0.029	-0.316	0.102	0.053	301	0.717
62	Delwood	18	-0.018	-0.081	0.148	0.126	127	0.454
63	Beaver	18	-0.036	-0.131	0.078	0.060	267	0.687
64	Robinson	18	0.068	-0.132	0.184	0.141	97	0.357
65	Shannon	4	0.039	NA	1.771	1.771	6	0.000
66	Caledonia	4	0	-0.318	0	0	0	0
67	Sherrard	4	-0.134	-0.598	0.270	0.068	234	0.653
68	Troy Grove	4	0.275	NA	0.622	0.622	0	0
69	Seneca	4	0.173	-0.608	0.120	0.029	0	0
70	Camp Point	4	-0.201	0.799	0.027	0.238	67	0.226
71	Duncan Mills	4	-0.160	-0.824	0.174	0.017	952	0.900
72	Greenview	4	-0.015	-0.810	0.021	0.002	6,775	0.985
73	Le Roy	4	-0.402	-0.240	3.114	1.908	5	0.000
74	Eldred	4	-0.060	-1.000	0.260	0.000	>10,000	1.000
75	Nilwood	4	-0.316	0.337	0.277	0.558	29	0.030
76	Yale	4	0.137	-0.803	0.144	0.016	962	0.901
77	York	4	-0.708	-0.058	1.522	1.355	11	0.000
78	Darmstadt	4	0.173	-0.261	0.108	0.063	224	0.640
79	Brownville	4	-0.063	-0.856	8.749	0.679	24	0.014
80	Sandusky	4	0.092	0.914	0.069	1.535	8	0.000
81	Cave in Rock	4	0.020	-0.792	4.183	0.485	28	0.029

Appendix 5.B. Route-specific estimates for the rate of change (r_{d0}), serial correlation (ρ), variance in population rate of change (V_r, V_{re}), years to quasi-extinction (T_{qe}), and probability of persistence for the next 100 years for Illinois Department of Natural Resources Bobwhite Call Count Survey routes.

Route	n	r_{d0}	ρ	V_r	V_{re}	T_{qe}	P_{100}
Adams	25	0.190	0.482	1.309	3.747	18	0.004
Cass	20	-0.136	0.700^*	3.873	21.969	3	<0.001
Christian	15	0.075	-0.119	5.467	4.301	15	0.001
Clark	25	-0.013	0.150	0.518	0.700	93	0.342
Clay-Jasper	25	0.045	0.504^*	1.473	4.468	22	0.010
Clinton	24	-0.052	0.174	1.254	1.782	56	0.168
Crawford	24	0.017	0.592^*	0.413	1.612	61	0.196
Cumberland	25	0.012	0.276	1.926	3.398	29	0.033
Edwards	24	0.065	0.680^*	0.279	1.462	67	0.226
Effingham	22	0.090	-0.010	0.910	0.891	111	0.407
Fayette East	23	0.108	0.796^*	0.299	2.636	38	0.071
Fayette West	25	0.020	0.049	0.990	1.093	91	0.332
Franklin	23	0.053	0.587^*	0.792	3.037	33	0.047
Gallatin-	24	-0.035	0.690^*	4.318	23.577	4	<0.001
Greene	6	-0.102	-0.367	0.241	0.112	872	0.892
Hamilton	25	-0.015	0.318	1.371	2.651	38	0.070
Hancock	25	0.067	0.423^*	1.436	3.539	28	0.029
Henderson	23	0.139	0.234	2.434	3.922	25	0.020
Henry	10	0.693	0.538^*	0.824	2.741	36	0.064
Jackson	18	-0.193	0.326	1.400	2.755	36	0.064
Jefferson	25	-0.016	-0.001	1.204	1.201	83	0.300
Jersey	25	0.117	-0.623^*	0.406	0.094	1,051	0.909
Lawrence	23	-0.047	0.271	0.546	0.952	104	0.384
Macoupin	24	0.115	0.274	0.516	0.905	109	0.401
Madison	25	-0.077	0.442^*	1.040	2.687	37	0.068
Marion	25	0.037	0.416^*	1.161	2.815	36	0.060
Massac	25	0.067	0.466^*	1.057	2.898	34	0.054
McDonald-	24	-0.217	0.452^*	0.705	1.868	52	0.147
Monroe	24	0.112	0.313	0.701	1.339	74	0.257
Montgomery	23	0.136	-0.057	5.327	4.750	20	0.007
Morgan	20	0.173	0.256	1.592	2.689	37	0.066
Old Randolph	12	0.073	0.262	0.809	1.383	70	0.241
Peoria	23	0.214	0.303	0.855	1.597	62	0.198
Perry	19	-0.088	0.643^*	1.896	8.711	11	<0.001
Pike	25	0.022	0.194	1.104	1.637	58	0.179

Appendix 5.B. Continued.

Route	n	r_{d0}	ρ	V_r	V_{re}	T_{qe}	P_{100}
Pope/Johnson	25	-0.087	0.547^*	1.259	4.295	22	0.010
Pulaski	15	-0.050	0.381	0.681	1.518	53	0.150
Richland	25	0.083	0.801^*	0.359	3.256	30	0.034
Rock Island	15	0.304	0.123	0.226	0.289	335	0.742
Saline	25	-0.273	0.738^*	3.960	26.246	4	<0.001
Schuyler	10	-0.080	0.296	1.766	3.252	31	0.039
Shelby	18	-0.034	-0.021	0.450	0.431	226	0.643
St. Clair	23	0.086	-0.018	5.230	5.044	20	0.006
Union	25	-0.129	0.580^*	1.870	7.038	14	<0.001
Wabash	24	0.065	0.794^*	0.656	5.704	17	0.003
Warren	25	0.054	0.360	2.215	4.711	21	0.009
Washington	25	0.174	0.338	0.667	1.347	74	0.260
Wayne	25	0.033	0.569^*	1.528	5.557	18	0.004
White	24	0.133	0.660^*	0.345	1.685	59	0.186
Whiteside	15	0.166	-0.563^*	4.230	1.182	85	0.306
Williamson	18	-0.153	0.663^*	2.096	10.333	10	<0.001

Appendix 7.A. Environmental variables related to bobwhite abundance indices in univariate spatial linear models. The configuration variables were also assessed for specific land use classes (e.g., row crop, small grains, woods, and grassland). Details of the configuration variables are available in McGarigal and Marks (1995).

VARIABLES		ACRONYM	UNIT	SCALE (ha)	TYPE
Land Use	Class		ha	Site, 5, 50, 500, 5,000	Composition
	Urban				
	Rural & Suburban				
	Transportation				
	Row Crops				
	Small Grains				
	Woods				
	Grasslands				
	Water/Wetlands				
Land Use Variety (2ha)				Site	Composition
Mean Elevation (and Standard Deviation)			m	Site, 5, 50, 500, 5,000	Composition
Slope (and Standard Deviation)			degree	Site, 5, 50, 500, 5,000	Composition
Aspect (and Standard Deviation)			degree	Site, 5, 50, 500, 5,000	Composition
Largest Patch Index		LPI		5, 50, 500, 5,000	Configuration
Number of Patches		NP	number	5, 50, 500, 5,000	Configuration
Patch Density		PD	number/100 ha	5, 50, 500, 5,000	Configuration
Mean Patch Size		MPS	ha	5, 50, 500, 5,000	Configuration
Patch Size Standard Deviation		PSSD	ha	5, 50, 500, 5,000	Configuration
Patch Size Coefficient of Variation		PSCV	%	5, 50, 500, 5,000	Configuration
Total Edge		TE	m	5, 50, 500, 5,000	Configuration
Edge Density		ED	m/ha	5, 50, 500, 5,000	Configuration
Landscape Shape Index		LSI		5, 50, 500, 5,000	Configuration
Mean Shape Index		MSI		5, 50, 500, 5,000	Configuration
Mean Patch Fractal Dimension		MPFD		5, 50, 500, 5,000	Configuration
Area-Weighted Mean Patch Fractal Dimension		AWMPFD		5, 50, 500, 5,000	Configuration

Appendix 7.A. Continued.

VARIABLES	ACRONYM	UNIT	SCALE (ha)	TYPE
Total Core Area	TCA	ha	5, 50, 500, 5,000	Configuration
Number of Core Areas	NCA	number	5, 50, 500, 5,000	Configuration
Core Area Density	CAD	number/100 ha	5, 50, 500, 5,000	Configuration
Mean Core Area Per Patch	MCA1	ha	5, 50, 500, 5,000	Configuration
Core Area Standard Deviation	CASD1	ha	5, 50, 500, 5,000	Configuration
Core Area Coefficient of Variation	CACV1	%	5, 50, 500, 5,000	Configuration
Mean Area Per Disjunct Core	MCA2	ha	5, 50, 500, 5,000	Configuration
Disjunct Core Area Standard Deviation	CASD2	ha	5, 50, 500, 5,000	Configuration
Disjunct Core Area Coefficient of Variation	CACV2	%	5, 50, 500, 5,000	Configuration
Total Core Area Index	TCAI	%	5, 50, 500, 5,000	Configuration
Mean Core Area Index	MCAI	%	5, 50, 500, 5,000	Configuration
Mean Nearest Neighbor	MNN	m	5, 50, 500, 5,000	Configuration
Nearest Neighbor Standard Deviation	NNSD	m	5, 50, 500, 5,000	Configuration
Nearest Neighbor Coefficient of Variation	NNCV	%	5, 50, 500, 5,000	Configuration
Mean Proximity Index	MPI		5, 50, 500, 5,000	Configuration
Shannon's Diversity Index	SHDI		5, 50, 500, 5,000	Configuration
Simpson's Diversity Index	SIDI		5, 50, 500, 5,000	Configuration
Modified Simpson's Diversity Index	MSIDI		5, 50, 500, 5,000	Configuration
Patch Richness	PR		5, 50, 500, 5,000	Configuration
Patch Richness Density	PRD	number/100 ha	5, 50, 500, 5,000	Configuration
Relative Patch Richness	RPR	%	5, 50, 500, 5,000	Configuration
Shannon's Evenness Index	SHEI		5, 50, 500, 5,000	Configuration
Simpson's Evenness Index	SIEI		5, 50, 500, 5,000	Configuration
Modified Simpson's Evenness Index	MSIEI		5, 50, 500, 5,000	Configuration
Interspersion and Juxtaposition Index	IJI	%	5, 50, 500, 5,000	Configuration

Appendix 7.B. Evaluating other landscape models of Northern Bobwhite response.

Brady et al. (1993), Schairer (1999), Michener et al. (2000), and L. W. Burger (*personal communication*) examined bobwhite population response to landscape characteristics. Brady et al.'s (1993) study was conducted in Kansas, Schairer's (1999) in Virginia, Michener et al.'s (2000) in Georgia, and Burger et al.'s in Missouri. Brady et al.'s (1993) least absolute deviation regression models were:

Bobwhite Abundance = -0.52 + 52.3(% of County in Ponds) + 68.0(% Woods) +21.6(% Soybean) - 174.0(% Oats) + 0.004($\text{Distance}_{\text{Cropland}}$), and
Bobwhite Abundance = 1 + 78(% Woods) + 98.9($\text{Hay}_{\text{Native}}$) - 33.3($\text{Hay}_{\text{excluding Alfalfa}}$).

Schairer's (1999) model, based on dichotomizing the counts between a 0–1 birds counted group and a >1 birds counted group, was:

Pr(Group Membership) = $e^Y/(1 + e^Y)$, where Y = -1.422 + 0.0448(%Row Crop) - 0.0401(Mean Patch $\text{Size}_{\text{Deciduous Forest}}$).
Michener et al.'s (2000) linear regression model was:

Standardized Covey Density = 2.562 + 2.820(Mean Shape $\text{Index}_{\text{Agriculture}}$) + 0.373(Mean Patch $\text{Size}_{\text{Agriculture}}$) - 0.197(Mean Patch $\text{Size}_{\text{Agriculture}})^2$.

Burger et al.'s logistic regression model was:

Habitat Suitability Index = Pr(Use) = $e^Y/(1 + e^Y)$, where Y = 3.18(Landscape Shape $\text{Index}_{\text{Row Crop}}$) + 0.05(Edge $\text{Density}_{\text{Wood}}$) + 0.06(Edge $\text{Density}_{\text{Conservation Reserve Program}}$).

I used these models as a starting point for my analyses by assessing models with the same parameters (at each of 3 spatial scales) on the Illinois landscape. I explicitly tested the models of Michener et al. and Burger et al. because they had complementary models in the Illinois landscape. For instance, because lands enrolled in the Conservation Reserve Program were not mapped for the entire extent of data surveyed in this study (Weber 2000), I used grassland as a correlate when testing Burger et al.'s model. I modeled variables of agriculture configuration only for row crop and not small grain agriculture. Brady et al.'s models were configured based on county level agricultural statistics, which were not explicitly examined in the context of this study.

Schairer (1999) found little distinction between habitats when he dichotomized the response to reflect presence (≥1 bird counted) and absence (0 birds counted).

The logistic models of Burger et al. and the linear models of Michener et al. (2000) were significant across most scales of analyses (Table 7.B.1, 7.B.2). However, they were not relevant models describing bobwhite-habitat associations in the Illinois landscape as their AICc scores and Aikike weights suggested the models performed poorly compared to the final models I derived (ΔAICc's > 50).

The models of Burger et al. and Michener et al. (2000) were statistically suitable for modeling distribution and abundance of bobwhite in Illinois. However, model adequacy, or fit, was considerably less than for the models I derived. The Burger et al. model was developed for bobwhite in Missouri and thus should translate reasonably well to bobwhite in Illinois if general enough; however, at all scales, the Burger et al. model performed less well than the most parsimonious model I developed. It is clear though that elements in both models share great similarities. For instance, in the Illinois landscape, amount of woods in the landscape is highly related to the amount of woods edge ($r = 0.93$). There are dissimilarities as well. To account for large-scale discontinuities in the distribution of bobwhite, my model included variables associated with small grain rather than row crop agriculture.

The Michener et al. (2000) model was developed for bobwhite in Georgia and is not as complex a model as the linear model I developed. Therefore, it is not surprising that there may be substantial differences in the fit of the model for a more northerly population, modeled across a greater area and range of scales. There were similarities, in that, both models included terms describing shape and size of agricultural cover types.

While the developers of these models had some justification for selecting the variables included in their models, my results indicated a more thorough variable selection

Table 7.B.1. Parameters (Slope (SE), *t*-statistic, and *P*-values), log-likelihoods (ℒ) and Aikike's small-sample Information Criterion (AICc) from logistic models, at each of 4 scales, of Northern Bobwhite presence/absence in Illinois. Model variables were determined by L. W. Burger (*personal communication*) and presence was determined from North American Breeding Bird Survey data (n = 3,000).

Scale		Intercept	$\log_{10}(\mathrm{LSI}_{\text{Row Crop}})$	$\log_{10}(\mathrm{ED}_{\text{Woods}})$	$\log_{10}(\mathrm{ED}_{\text{Grass}})$	log(ℒ)	AICc
5 ha	β	-1.2159 (0.1240)	0.1567 (0.0725)	0.0028 (0.0005)	0.0009 (0.0004)	-144.1	-288.2
	t	-9.81	2.16	4.79	2.06		
	P	<0.0001	0.7254	<0.0001	0.0393		
50 ha	β	-2.0622 (0.1693)	0.5092 (0.0683)	0.0087 (0.0009)	0.0001 (0.0008)	-128.4	-256.7
	t	-12.18	7.46	9.38	0.14		
	P	<0.0001	<0.0001	<0.0001	0.8879		
500 ha	β	-3.0106 (0.1722)	0.5698 (0.0470)	0.0259 (0.0018)	-0.0101 (0.0017)	-86.5	-173.0
	t	-17.49	12.12	14.51	-5.96		
	P	<0.0001	<0.0001	<0.0001	<0.0001		

Table 7.B.1. Continued.

Scale		Intercept	$\log_{10}(\mathrm{LSI}_{\text{Row Crop}})$	$\log_{10}(\mathrm{ED}_{\text{Woods}})$	$\log_{10}(\mathrm{ED}_{\text{Grass}})$	$\log(\mathcal{L})$	AICc
5,000 ha	β	-3.2701 (0.1842)	0.2301 (0.0189)	0.0455 (0.0024)	-0.0172 (0.0021)	-59.3	-118.6
	t	-17.75	12.17	18.62	-8.03		
	P	<0.0001	<0.0001	<0.0001	<0.0001		

Table 7.B.2. Parameters (Slope (SE), *t*-statistic, and *P*-values), log-likelihoods ($\mathcal{L}$) and Aikike's small-sample Information Criterion (AICc) for linear models, applied at each of 4 scales, to North American Breeding Bird Survey data ($n = 2{,}295$) for Northern Bobwhite in Illinois. Model variables determined by Michener et al. (2000); response is the mean count, detrended and transformed, from 1985–1998.

Scale		Intercept	$\mathrm{MSI}_{\mathrm{Row\ Crop}}$	$\mathrm{MPS}_{\mathrm{Row\ Crop}}$	$\mathrm{MPS}^2_{\mathrm{Row\ Crop}}$	$\log(\mathcal{L})$	AICc
5 ha	β	0.7776 (0.0225)	0.0002 (0.0072)	0.0092 (0.0039)	-0.0013 (0.0007)	-2,643.7	5,287.5
	t	34.59	0.02	2.35	-1.82		
	P	<0.0001	0.9825	0.0187	0.0684		
50 ha	β	0.7663 (0.0221)	0.0114 (0.0050)	0.0010 (0.0004)	<0.0001 (0.0001)	-2,640.1	5,280.2
	t	34.74	2.30	2.40	-2.82		
	P	<0.0001	0.0213	0.0166	0.0049		
500 ha	β	0.7661 (0.0228)	0.0170 (0.0054)	-0.0001 (0.0001)	<0.0001 (0.0001)	-2,642.8	5,285.6
	t	33.63	3.17	-2.04	0.63		
	P	<0.0001	0.0016	0.0413	0.5256		

Table 7.B.2. Continued.

Scale		Intercept	$\text{MSI}_{\text{Row Crop}}$	$\text{MPS}_{\text{Row Crop}}$	$\text{MPS}^2_{\text{Row Crop}}$	log($\mathscr{L}$)	AICc
5,000 ha	β	0.7064 (0.0317)	0.0552 (0.0153)	-0.0001 (0.0001)	<0.0001 (0.0001)	-2,639.7	5,279.5
	t	22.30	3.61	-2.58	0.58		
	P	<0.0001	0.0003	0.0100	0.5633		

procedure is generally warranted, at least until theory or empirical evidence has been well established allowing proper dismissal of spurious variables (Guthery 1997). There were large collinearities between many of the configuration variables included in each of the models. Shannon's Evenness Index (occurring in the logistic model) and the various edge indices included in Burger et al., as well as variation in row crop core size (linear model) and row crop patch size (Michener et al. 2000) were highly collinear. Determining the mechanisms by which these landscape configuration variables directly influence bobwhite population dynamics, if they truly do, is clearly important.

Appendix 7.C. From an Information Theoretic perspective, the influence of environmental and historical parameters on presence/absence of Northern Bobwhite in Illinois, as determined from North American Breeding Bird Survey data ($\log(\mathscr{L}) = 469.1$, pseudo-$R^2 = 0.455$).

Parameter	β	SE	*t*	*P*
Intercept	4.698	2.232	2.10	0.0353
$\log_{10}$(Small Grain$_{5,000\ \mathrm{ha}}$)	1.969	0.139	14.14	<0.0001
$\log_{10}$(Shannon's Evenness Index)	-2.183	0.873	-2.50	0.0124
$\log_{10}$(Elevation$_{5,000\ \mathrm{ha}}$)	-7.866	0.790	-9.96	<0.0001
$\log_{10}$(Woods$_{5,000\ \mathrm{ha}}$)	0.501	0.094	5.32	<0.0001
Total Winter Snow, 1977	-0.013	0.005	-2.70	0.0069
Total Winter Snow, 1979	0.007	0.002	3.32	0.0009
Mean Spring Precipitation, 1977	-0.011	0.004	-2.96	0.0031
Mean Spring Precipitation, 1978	0.013	0.005	2.57	0.0102

Appendix 7.D. Equations for relevant configuration variables.

Shannon's Evenness Index

$$J' = -\sum_{i=1}^{m} (P_i \times \ln P_i) \Big/ \ln m$$

Landscape Shape Index

$$LSI = \frac{0.25 \sum_{k=1}^{m} e''_{ik}}{\sqrt{A}}$$

Mean Core Area per Patch

$$MCA1 = \frac{\sum_{j=1}^{n} a_{ij}^{c}}{n_i} \left(\frac{1}{10{,}000} \right)$$

Class Area Coefficient of Variation

$$CACV1 = \frac{\sqrt{\frac{\sum_{j=1}^{n} \left[a_{ij}^{c} - \left(\frac{\sum_{j=1}^{n} a_{ij}^{c}}{n_i} \right) \right]^2}{n_i}} \left(\frac{1}{10{,}000} \right)}{MCA1} (100)$$

Total Core Area Index

$$TCAI = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}^{c}}{A}(100)$$

Mean Core Area Index

$$MCAI = \frac{\sum_{j=1}^{n} a_{ij}^{c}}{n_i}\left(\frac{1}{10{,}000}\right)$$

Mean Nearest Neighbor

$$MNN = \frac{\sum_{j=1}^{n'} h_{ij}}{n'_i}$$

Mean Proximity Index

$$MPI = \frac{\sum_{j=1}^{n}\sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^{2}}}{n_i}$$

Mean Area per Disjunct Core

$$MCA2 = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\sum_{q=1}^{p} a_{ijq}^{\;c}}{\sum_{i=1}^{m}\sum_{j=1}^{n} n_{ij}^{c}}\left(\frac{1}{10{,}000}\right)$$

Interspersion and Juxtaposition Index

$$IJI = \frac{-\sum_{k=1}^{m'} \left[\left(\frac{e_{jk}}{\sum_{k=1}^{m'} e_{jk}} \right) \ln \left(\frac{e_{jk}}{\sum_{k=1}^{m'} e_{jk}} \right) \right]}{\ln(m'-1)} (100)$$

Core Area Percentage of Landscape

$$CLAND = \frac{\sum_{j=1}^{n} a_{ij}^{c}}{A} (100)$$

Appendix 9. Location (Universal Transverse Mercator coordinates of the patch centroid), network identifier, number of neighbors within network, proportion of those neighbors predicted to be unoccupied or sparsely occupied, patch size, and mean landscape suitability (HSI) for patches potentially suited for translocation. Variable-specific rankings are provided parenthetically for the first 26 patches.

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
1	281034.2	4496541.7 (6)	25	254 (1)	0.286 (115)	1,497.6 (24)	0.545 (7)
2	288617.2	4504734.4 (14)	25	254 (1)	0.286 (115)	2,319.7 (19)	0.538 (15)
3	176300.0	4563604.7 (44)	25	254 (1)	0.286 (115)	9483.1 (7)	0.554 (4)
4	285119.0	4480718.9 (2)	25	254 (1)	0.286 (115)	877.4 (32)	0.532 (23)
5	331079.6	4580595.0 (72)	25	254 (1)	0.286 (115)	32,508.1 (1)	0.611 (1)
6	164404.4	4564798.6 (45)	25	254 (1)	0.286 (115)	694.0 (34)	0.534 (19)
7	160362.6	4571367.1 (58)	25	254 (1)	0.286 (115)	2,589.8 (16)	0.530 (25)
8	291605.9	4588150.9 (79)	25	254 (1)	0.286 (115)	3,753.8 (11)	0.540 (14)
9	281405.1	4529871.6 (18)	25	254 (1)	0.286 (115)	66.5 (72)	0.533 (21)
10	246622.2	4501170.1 (9)	25	254 (1)	0.286 (115)	87.9 (64)	0.520 (39)
11	169346.0	4550438.1 (26)	25	254 (1)	0.286 (115)	160.7 (53)	0.520 (37)
12	281177.5	4493919.1 (5)	25	254 (1)	0.286 (115)	62.2 (75)	0.520 (41)
13	288846.5	4541395.7 (20)	25	254 (1)	0.286 (115)	158.0 (55)	0.518 (46)
14	352335.8	4589719.1 (80)	24	4 (149)	1.000 (1)	2,663.3 (15)	0.545 (8)
15	177993.2	4570281.3 (54)	25	254 (1)	0.286 (115)	248.3 (43)	0.520 (42)
16	298828.3	4695139.8 (153)	3	11 (90)	1.000 (1)	15,746.6 (4)	0.541 (11)
17	420675.6	4548722.4 (22)	36	28 (74)	0.379 (102)	1,081.8 (29)	0.521 (34)
18	270567.2	4571536.0 (59)	25	254 (1)	0.286 (115)	402.2 (36)	0.517 (52)
19	408511.5	4555708.5 (33)	36	28 (74)	0.379 (102)	3,262.3 (14)	0.520 (40)
20	238008.5	4550745.3 (27)	39	1 (179)	1.000 (1)	1,420.4 (26)	0.522 (33)
21	288122.4	4512746.5 (15)	25	254 (1)	0.286 (115)	35.6 (93)	0.519 (45)
22	273683.2	4527267.9 (17)	25	254 (1)	0.286 (115)	73.6 (71)	0.513 (69)
23	279142.7	4699492.8 (162)	2	10 (102)	1.000 (1)	11,175.8 (5)	0.537 (17)
24	262064.1	4620710.9 (113)	15	4 (149)	1.000 (1)	3,558.9 (13)	0.541 (12)
25	209875.9	4561029.6 (39)	37	0 (191)	1.000 (1)	972.8 (31)	0.529 (26)
26	304282.8	4580075.2 (70)	25	254 (1)	0.286 (115)	56.4 (78)	0.523 (30)

Appendix 9.A. Continued.

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
27	361665.9	4599981.4	24	4	1.000	1,723.4	0.529
28	228095.8	4593413.4	27	8	0.889	6,402.7	0.552
29	240257.1	4587402.4	27	8	0.889	2,386.1	0.545
30	355506.1	4539208.7	40	1	0.500	10,860.4	0.545
31	287336.0	4542037.8	25	254	0.286	31.3	0.512
32	173744.9	4570081.8	25	254	0.286	79.6	0.512
33	277302.0	4639646.5	9	4	1.000	3,875.4	0.528
34	169244.5	4578451.1	30	8	0.778	1,033.9	0.535
35	342604.1	4602633.6	22	0	1.000	2,218.2	0.542
36	167557.7	4586358.4	30	8	0.778	1,458.1	0.538
37	358780.3	4592518.7	24	4	1.000	294.8	0.518
38	350862.5	4596970.4	24	4	1.000	242.4	0.519
39	416099.5	4550118.4	36	28	0.379	85.1	0.515
40	372242.2	4609751.9	19	0	1.000	2,496.6	0.534
41	276221.0	4514833.4	25	254	0.286	22.2	0.510
42	270457.5	4633290.8	9	4	1.000	845.2	0.523
43	305891.5	4663224.4	6	10	0.636	16,481.0	0.563
44	247863.5	4499474.9	25	254	0.286	25.6	0.509
45	173334.5	4567108.4	25	254	0.286	91.5	0.509
46	282462.5	4698414.5	2	10	1.000	379.7	0.519
47	303230.6	4638989.5	6	10	0.636	3,935.9	0.541
48	227029.9	4573468.1	32	0	1.000	379.5	0.516
49	313213.7	4622146.3	14	0	1.000	1,792.9	0.532
50	411613.6	4559882.2	36	28	0.379	93.9	0.512
51	294542.1	4490868.2	49	5	0.333	380.6	0.517
52	244894.5	4626508.9	13	7	1.000	196.1	0.517
53	304590.9	4576291.5	25	254	0.286	7.3	0.521
54	309680.0	4647977.9	6	10	0.636	3,632.8	0.532

Appendix 9.A. Continued.

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
55	248548.9	4613805.9	18	0	1.000	2,146.0	0.518
56	221882.9	4591668.9	27	8	0.889	160.4	0.521
57	302173.2	4598651.9	26	4	1.000	183.2	0.512
58	305807.3	4598396.2	26	4	1.000	341.8	0.512
59	269277.9	4697983.5	2	10	1.000	191.3	0.515
60	292944.6	4548887.3	25	254	0.286	8.1	0.511
61	217549.1	4570234.9	25	254	0.286	24.7	0.510
62	253791.5	4577775.8	25	254	0.286	27.6	0.511
63	287527.6	4480118.1	25	254	0.286	8.8	0.509
64	300063.4	4693033.1	3	11	1.000	62.0	0.513
65	291171.9	4504423.4	25	254	0.286	5.3	0.511
66	339415.5	4574362.8	25	254	0.286	21.4	0.511
67	181251.8	4570128.0	25	254	0.286	29.7	0.509
68	310062.1	4693496.2	4	1	1.000	1,216.5	0.523
69	251327.0	4602909.4	23	0	1.000	181.0	0.518
70	303130.4	4549720.3	25	254	0.286	7.8	0.510
71	297026.0	4577282.2	25	254	0.286	11.9	0.511
72	188905.0	4561184.2	25	254	0.286	47.8	0.507
73	163858.8	4584318.6	30	8	0.778	162.8	0.514
74	337511.3	4573173.5	25	254	0.286	5.2	0.514
75	247064.0	4503373.3	25	254	0.286	4.3	0.510
76	316214.4	4571317.6	25	254	0.286	6.0	0.512
77	322915.5	4655585.1	8	1	1.000	229.2	0.518
78	250779.5	4503560.3	25	254	0.286	11.4	0.507
79	237495.7	4580180.2	27	8	0.889	85.0	0.513
80	385264.0	4609059.1	21	2	1.000	221.7	0.511
81	296557.3	4704585.9	3	11	1.000	82.1	0.512
82	339348.8	4575290.4	25	254	0.286	11.6	0.510

Appendix 9.A. Continued.

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
83	308023.3	4704184.0	3	11	1.000	42.4	0.514
84	280979.3	4663131.5	7	1	1.000	201.3	0.518
85	258275.4	4616106.3	15	4	1.000	65.8	0.512
86	223987.6	4699371.5	1	21	0.227	27,895.8	0.601
87	302893.3	4699871.7	3	11	1.000	43.9	0.512
88	231508.0	4613727.9	17	1	1.000	52.9	0.516
89	217020.1	4571327.3	25	254	0.286	7.6	0.510
90	172521.9	4577805.3	30	8	0.778	46.2	0.513
91	265953.3	4562577.8	33	3	0.250	1,314.6	0.528
92	169453.8	4592477.6	30	8	0.778	102.1	0.512
93	245049.5	4628449.8	13	7	1.000	86.6	0.510
94	174606.5	4570570.0	25	254	0.286	11.9	0.507
95	245024.9	4630857.5	13	7	1.000	37.5	0.512
96	257159.0	4617380.7	15	4	1.000	89.5	0.509
97	276403.9	4700012.6	2	10	1.000	17.7	0.515
98	245355.5	4625195.4	13	7	1.000	13.8	0.513
99	182789.8	4570094.4	25	254	0.286	11.5	0.507
100	302245.4	4684766.4	3	11	1.000	40.7	0.509
101	308897.8	4703588.4	3	11	1.000	32.5	0.511
102	408620.4	4559270.0	36	28	0.379	21.8	0.508
103	314685.6	4646018.0	6	10	0.636	89.5	0.516
104	416073.1	4551971.8	36	28	0.379	16.5	0.508
105	304232.5	4670800.8	6	10	0.636	157.2	0.515
106	164415.5	4586440.2	30	8	0.778	13.8	0.517
107	241654.5	4498388.2	25	254	0.286	4.7	0.506
108	291421.1	4583335.1	25	254	0.286	5.8	0.510
109	187073.2	4504223.3	25	254	0.286	4.4	0.506
110	243556.9	4624376.5	13	7	1.000	58.6	0.508

Appendix 9.A. Continued.

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
111	275754.7	4693217.8	2	10	1.000	48.6	0.508
112	238077.1	4594326.4	27	8	0.889	47.3	0.510
113	244256.7	4625127.5	13	7	1.000	53.8	0.508
114	265976.4	4567415.4	33	3	0.250	136.4	0.520
115	232674.9	4616757.6	17	1	1.000	29.4	0.511
116	296960.9	4705906.6	3	11	1.000	33.0	0.509
117	412088.8	4561533.7	36	28	0.379	19.2	0.507
118	237733.0	4579470.7	27	8	0.889	41.3	0.508
119	243036.1	4567101.7	35	0	1.000	11.8	0.509
120	235330.7	4593214.1	27	8	0.889	32.5	0.510
121	179622.8	4593763.9	29	0	1.000	9.6	0.513
122	323372.1	4601630.5	25	254	0.286	10.4	0.508
123	326066.9	4622236.8	16	0	1.000	26.1	0.512
124	290992.1	4681887.3	3	11	1.000	14.1	0.508
125	306522.4	4597853.4	26	4	1.000	14.5	0.508
126	415529.0	4554860.0	36	28	0.379	9.7	0.507
127	186677.2	4562714.0	25	254	0.286	4.2	0.507
128	236339.9	4589900.9	27	8	0.889	14.3	0.511
129	381667.5	4610699.1	21	2	1.000	50.1	0.508
130	269804.3	4560775.2	33	3	0.250	125.4	0.515
131	303687.5	4699941.2	3	11	1.000	8.9	0.511
132	158259.5	4570219.3	25	254	0.286	5.5	0.506
133	320367.5	4657714.0	8	1	1.000	45.2	0.511
134	256498.2	4618808.1	15	4	1.000	16.3	0.509
135	302925.5	4692954.0	3	11	1.000	8.3	0.509
136	417068.0	4552297.8	36	28	0.379	8.4	0.507
137	269620.4	4681374.5	1	21	0.227	415.6	0.513
138	354290.7	4674917.9	5	0	1.000	86.6	0.510

Appendix 9.A. Continued.

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
139	303622.7	4597977.9	26	4	1.000	17.2	0.507
140	415215.5	4554216.2	36	28	0.379	9.0	0.506
141	313079.8	4695290.7	4	1	1.000	50.0	0.511
142	289410.2	4633791.7	12	2	0.667	288.9	0.513
143	243321.1	4625409.0	13	7	1.000	32.9	0.506
144	235283.4	4551179.5	39	1	1.000	7.3	0.506
145	244135.4	4623695.4	13	7	1.000	4.1	0.511
146	412367.0	4560412.1	36	28	0.379	5.6	0.507
147	274709.1	4705581.6	2	10	1.000	6.1	0.510
148	357514.6	4590235.4	24	4	1.000	4.3	0.508
149	269979.5	4695738.3	2	10	1.000	11.5	0.507
150	265317.2	4619574.6	15	4	1.000	18.7	0.507
151	273187.6	4694598.2	2	10	1.000	8.1	0.508
152	266953.9	4611965.5	20	0	1.000	24.5	0.508
153	323600.2	4600958.9	25	254	0.286	4.6	0.506
154	303202.0	4597470.0	26	4	1.000	6.0	0.507
155	269621.5	4695339.3	2	10	1.000	5.2	0.508
156	293520.5	4487973.3	49	5	0.333	6.3	0.507
157	165118.9	4583309.9	30	8	0.778	4.1	0.509
158	294268.9	4697647.0	3	11	1.000	7.0	0.506
159	266607.0	4630010.4	9	4	1.000	10.6	0.506
160	268132.5	4699794.2	2	10	1.000	5.4	0.507
161	279017.0	4646444.1	9	4	1.000	8.5	0.507
162	286695.8	4632705.9	12	2	0.667	64.2	0.510
163	269360.7	4635253.6	9	4	1.000	7.4	0.507
164	280724.5	4660312.8	7	1	1.000	15.9	0.507
165	267648.0	4697687.6	2	10	1.000	7.2	0.506
166	220423.3	4689441.3	1	21	0.227	12.4	0.515
167	381222.4	4610369.1	21	2	1.000	4.6	0.508

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