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COOPERATIVE UPLAND WILDLIFE RESEARCH AND SURVEYS

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W-106-R-12 Volume 1

COOPERATIVE UPLAND WILDLIFE RESEARCH AND SURVEYS

FINAL REPORT

VOLUME 1 OF 2

Federal Aid Project W-106-R-12

Submitted by:

Cooperative Wildlife Research Laboratory, SIUC

Presented to:

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June 2002

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COOPERATIVE WILDLIFE RESEARCH LABORATORY

FINAL REPORT - VOLUME 1

<u>**STATE OF ILLINOIS**</u>

<u>**W-106-R (10-12)**</u>

Project Period: 1 July 1999 through 30 June 2001

Project: Cooperative Upland Wildlife Research and Surveys (Phase IV)

STUDY R-1. UPLAND WILDLIFE/HABITAT RELATIONSHIPS

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EXECUTIVE SUMMARY

This Federal Aid Project consists of 2 studies that are distinct enough to warrant reporting in separate volumes, hence the organization of this Final Performance Report. This volume (1) reports on the findings of Study R-1 (Upland Wildlife/Habitat Relationships). Study R-2 (Population Dynamics and Status of the Swamp Rabbit in Illinois) is reported in Volume 2. Following is a summary of findings of the 2 jobs in Study R-1.

Job R-1.1: Conservation Reserve Program

The objective of this job was to inventory CRP practices (amount, type, distribution) in southern and west-central Illinois and evaluate their contribution to upland wildlife habitat. Data collection entailed digital mapping of geographic locations and acquisition of associated attribute data (sign-up period, contract year, acreage enrolled, status of contract, and cover practice [CP]) of active individual CRP fields within the boundaries of study counties through Sign-up 19. Spatial and statistical analyses were conducted to determine the type of landscape in which CRP fields were located and their influence on landscape composition and structure.

Farmland enrolled in CRP tended to be located in areas with proportionately less row crop, but more grassland and woodland, than non-CRP landscapes. Patch size and core areas of row crop, grassland, and woodland patches were consistently smaller within CRP landscapes, and consequently, edge density was greater in CRP landscapes. Landscapes surrounding CRP fields were less contiguous and more diverse than were non-CRP landscapes.

Landscapes surrounding CRP following Sign-up 14 ("new" CRP) contained larger mean patch sizes of grassland and correspondingly lower edge and path densities, and greater core areas than did CRP fields that entered the program prior to Sign-up 14 ("old" CRP). This suggests that the "new" CRP (71.2% of the CRP within the study area) has a greater potential to benefit area sensitive grassland birds than did the "old" CRP. Inclusion of CRP in the landscape resulted in even greater proportions of grassland and woodland than were previously present, while proportions of row crop decreased further. Thus, CRP contributed to greater overall size of grassland and woodland patches while row crop patch size decreased. Edge density decreased overall and within row crop patches, but increased in grassland and woodland patches. Neither contagion nor evenness were influenced by CRP enrollment.

Conversion of lands from row crop production to semi-permanent grass or tree plantings in effect added grasslands and woodlands to those areas already containing relatively more of these land cover types than the county landscape in general. If increasing grassland patch sizes for area-sensitive grassland bird species is the main objective of habitat improvement efforts, then CRP as currently located may achieve the goal if sufficient acreage can be added to the landscape. If however, the goal is to add grassland acreage to areas lacking this cover type, constraints as to where CRP may be placed (e.g., eligible lands and landowner desire to participate) must be overcome. Unfortunately, freedom of CRP placement is the ideal rather than reality, so the alternative to maximize benefits is to consider what CP will provide the most wildlife benefits in a given landscape. Then, every effort must be made to maintain fields to maximize desired wildlife habitat benefits.

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Job R-1.2: Landscape/Site Level Bobwhite Habitat

Objectives were to (1) investigate relationships between bobwhite distribution/abundance and habitat at the landscape and site level; (2) identify limiting components in unoccupied or sparsely populated areas and evaluate the feasibility of restoring them; and (3) examine relationships between population parameters, observed population decline, and seasonal climatological conditions. Three models were created to address this job's first objective. 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 land that could be potentially occupied. The difference of these 2 maps defined areas of Illinois devoid of bobwhite, but which were suitable for occupancy. The third model, the spatial linear model, described extant abundance in Illinois. 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. Based on NABBS count data, mean probability of occupation was 0.55 ± 0.01. The mean model at HSI = 0.50 predicted 71,294 km^2 (48.9% of the state) of potentially suitable habitat for bobwhite. The suitability of habitat dropped off quickly, with little habitat at HSI > 0.80 and virtually none at HSI > 0.90. 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.

Projections of potential fall bobwhite population size were undoubtedly too high when estimates of birds/ha were applied to the 71,294 km^2 predicted suitable landscape. Clearly adequate site-level habitat exists only as patches with the predicted suitable landscape; we

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hypothesize this may amount to only 37.5% of suitable landscape acreage. Also, another model of bobwhite habitat suitability (Roseberry and Sudkamp 1998) with a more patchy configuration predicted less (35,000 vs 71,294 km^2) suitable landscape throughout the state which further illustrates the importance of site-level habitat quality within a suitable landscape.

The second objective was addressed with models that incorporated documented bobwhite dispersal movements and related these to habitat distribution and colonization/extinction probability. We hypothesized the bobwhite in Illinois dispersed a median distance of 1.5 km and a maximum distance of 35.3 km. Bobwhite habitat in Illinois consisted of 416 patches >4 ha occurring in 52 networks. Available habitat was dominated by 1 patch that included 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. Analysis suggested virtually no patch in Illinois was >17 km from another suitable patch of optimal habitat. However, 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).

It may be that the rather sedentary nature of bobwhite allow extinctions to occur at greater than historical frequencies (and at a greater rate than colonizations) due to anthropogenic causes. Large grassland patches that lacked sufficient woody cover increased probability of bobwhite extirpation in a landscape. The amount of landscape devoted to human habitation also was a factor associated with bobwhite extirpation. 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, probability of colonization increased.

Areas with potential for restoration were identified. The top 2 patches for possibly translocating northern bobwhite based on ecological criteria were in Tazewell County adjacent to

the large contiguous patch of occupied habitat ("mainland") occurring throughout western and southern Illinois . 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. Each of the top choices are associated with nearby occupied habitats. Thus, an important reason for a depauperate patch may either be the lack of suitable site-level habitat, or the lack of dispersal corridors between occupied and unoccupied habitat.

The third objective entailed analyses of a 50-year sample ($n = 183{,}264$) of bobwhite wings collected by hunters in the 34 southernmost Illinois counties. We used these wing-derived data to examine potential relationships between age- and sex-structure and temporal patterns in abundance. We then discerned relationships between biological response parameters (intrinsic factors), and climatological information and historical agricultural data (extrinsic factors). There were no obvious, long-term trends in sex ratios among juveniles or adults; annual fluctuations were minor and seemingly unrelated to climatological or habitat conditions, and may therefore have simply reflected random variation. Sex ratios seemed unrelated to other population parameters except for a weak tendency for declining populations to contain slightly more males among juveniles.

Hatching chronology, as indexed by the relative proportion of late-hatched juveniles in the fall population, increased from 1950 through the 1970's then stabilized. Because late clutches are generally smaller, reliance on renesting to compensate for failure of initial attempts could theoretically reduce productivity. Indeed, late hatches were often associated with annual population declines, and vice versa.

The ratio of juveniles per adult in fall populations declined from 1950 to about 1970, then stabilized over the remainder of the study. This trend was statistically associated with changes in gross amounts of agricultural grasslands (i.e., nesting cover) throughout the state and thus appeared habitat related. The fact that populations declined over the last 30 years of study

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whereas juveniles per adult (JPA) was relatively stable suggests habitat loss rather than deterioration. In contrast, declining JPA during the first 20 years of study may have reflected habitat deterioration prior to complete elimination. Annual variation in this parameter was weather related with above-average summer precipitation and harsh winters leading to higher ratios. The latter relationship, which initially seems illogical, probably reflects the density-dependent nature of JPA and the fact that severe winters often were followed by very low breeding densities. Because JPA was strongly density-dependent, and integrated a variety of biological variables, the parameter was not a particularly good indicator of relative or absolute productivity or subsequent population size.

Literature Cited

Roseberry, J. L., and S. D. Sudkamp. 1998. Assessing the suitability of landscapes for northern bobwhite. Journal of Wildlife Management 62:895-902.

Problem: Certain conservation provisions of the 1996 Farm Bill provide opportunity to create and enhance upland wildlife habitat in Illinois. To better exploit these opportunities, information is needed regarding the amount, distribution, and cover practices associated with new and re-enrolled Conservation Reserve Program (CRP) areas. It would also be desirable to obtain similar information about acres that have been removed from the program. In addition, better understanding of the relationship between site and landscape conditions is necessary to intelligently recommend specific site practices to maximize potential benefits for species such as the northern bobwhite.

Objectives:

1. To inventory CRP practices (amount, type, distribution) in southern and west-central Illinois and evaluate their contribution to upland wildlife habitat.

2. To investigate relationships between bobwhite distribution/abundance and habitat at the landscape and site level.

3. To identify limiting habitat components and landscape features in areas unoccupied or sparsely populated by bobwhite and evaluate the feasibility of restoring them.

JOB R-1.1 CONSERVATION RESERVE PROGRAM

Objective: To inventory CRP practices (amount, type, distribution) in southern and west-central Illinois and evaluate their contribution to upland wildlife habitat.

A thesis by Weber (2000) is attached in lieu of a final report for this job. In addition to data presented in the thesis, we calculated total CRP acreage within Illinois (Table 1) from Sign-up 15 (accepted plus remaining acres beginning FY 1998) and including cumulative acreage as of October 2000.   Continuous, CREP (Conservation Reserve Enhancement Program), Appeals, and Waivers (Sign-ups 14, 17, and 19) are not included in the total.

Following is the abstract of Weber's (2000) thesis:

The Conservation Reserve Program (CRP) has been converting environmentally sensitive acreage from agricultural production to semi-permanent vegetative cover since

1986. Agriculture comprises > 80% of overall land use in Illinois and CRP could have a profound impact on both landscape composition and structure. I recorded geographic locations and associated attribute data for all CRP fields within 11 selected counties in west-central and southern Illinois. Locations of CRP fields recorded on 1:12,000 scale black and white aerial photographs were used to create digitized land cover images on county maps, and in the calculation of landscape metrics. Land enrolled in CRP tended to be situated in landscapes characterized by small patches, greater edge density and diversity, and consequently greater fragmentation than the general county landscape. The results indicate conversion of lands from row crop production to semi-permanent grass or tree plantings is in effect adding grass- and woodlands to areas already containing relatively more of these landcover types than the county landscape in general. By replacing cropland with CRP, a decrease in the proportion, patch size, and edge density of row crop was affected, concurrent with an increase in the proportion, patch size, and edge density of grassland and woodland. If CRP is to positively impact wildlife, land managers and wildlife biologists must collaborate to determine which wildlife benefits to concentrate efforts on, and where CRP should be located to maximize desired landscape effects. If increasing grassland patch sizes for area-sensitive grassland bird species is the main objective of habitat improvement efforts, then CRP as currently located may achieve this goal if sufficient CRP is added to the landscape. However, if the goal is to create new habitat by adding grassland acreage to areas that lack this cover type, then greater forethought must go into the placement of CRP fields.

Table 1. Conservation Reserve Program (CRP) acreage within Illinois beginning FY1998 through October 2000 (excluding Continuous, CREP, Appeals, and Waivers).

COUNTY	Signup 15[a]	Signup 16[b]	Signup 18[c]	Signup 20[d]
ADAMS	9,443	14,768	15,731	17,382
ALEXANDER	263	294	294	1,019
BOND	8,741	8,125	9,555	12,159
BOONE	653	997	850	847
BROWN	8,712	9,411	10,901	14,292
BUREAU	2,321	3,666	4,462	6,078
CALHOUN	6,494	7,001	8,048	8,981
CARROLL	6,804	7,505	7,880	9,087
CASS	3,724	4,261	5,967	10,491
CHAMPAIGN	3,359	4,609	5,018	6,495
CHRISTIAN	1,853	1,979	2,317	3,602
CLARK	1,142	4,658	5,108	5,683
CLAY	9,597	9,817	10,979	12,454
CLINTON	1,842	1,994	2,700	4,820
COLES	2,356	2,551	2,840	3,760
CRAWFORD	1,230	5,862	5,992	8,672
CUMBERLAND	1,831	2,698	3,006	4,436
DEKALB	369	884	1,233	2,073
DEWITT	389	830	795	1,231
DOUGLAS	929	2,217	2,986	3,618
EDGAR	5,590	4,372	3,530	4,627
EDWARDS	5,440	5,029	5,198	6,363
EFFINGHAM	2,603	4,002	4,653	6,209
FAYETTE	15,819	12,627	13,402	14,708
FORD	1,732	2,866	3,605	4,568
FRANKLIN	20,228	22,707	23,435	24,200
FULTON	3,103	3,406	3,784	6,774
GALLATIN	1,332	2,421	2,857	3,392
GREENE	6,508	7,442	7,140	7,496
GRUNDY	25	579	739	918
HAMILTON	25,217	27,247	28,654	31,512
HANCOCK	10,289	12,888	13,510	17,143
HARDIN	2,898	2,865	2,413	2,687
HENDERSON	904	848	736	974
HENRY	8,979	9,567	10,571	12,728
IROQUOIS	4,385	7,178	6,799	12,175
JACKSON	7,495	9,114	9,976	11,654
JASPER	2,457	3,531	4,506	6,117
JEFFERSON	31,232	31,702	32,242	33,999
JERSEY	5,338	5,736	5,402	5,670
JO DAVIESS	25,345	25,039	25,083	27,121
JOHNSON	15,237	15,652	16,736	17,983
KANE	87	150	115	137
KANKAKEE	638	1,129	1,196	1,520

Table 1. Continued.

COUNTY	Signup 15[a]	Signup 16[b]	Signup 18[c]	Signup 20[d]
KENDALL	451	339	347	366
KNOX	4,592	4,965	5,287	9,144
LAKE		4,676	33	0
LA SALLE	5,214		4,281	5,117
LAWRENCE	5,714	4,983	5,025	5,827
LEE	688	1,253	1,704	2,712
LIVINGSTON	4,218	4,119	3,332	6,597
LOGAN	984	1,570	1,847	3,866
MCDONOUGH	1,846	3,095	3,012	4,548
MCHENRY	1,724	2,432	2,101	2,227
MASON	6,111	4,932	8,154	6,714
MACON	781	1,028	1,008	1,145
MACOUPIN	8,400	8,576	8,915	10,672
MADISON	4,005	3,655	3,425	3,521
MARION	22,247	23,222	26,874	30,707
MARSHALL	571	879	1,044	1,225
MASSAC	7,985	8,077	8,006	10,110
MCLEAN	6,553	7,769	5,452	9,336
MENARD	2,043	2,747	3,363	3,917
MERCER	8,115	8,782	8,588	10,005
MONROE	5,200	4,557	4,570	4,341
MONTGOMERY	7,823	8,387	9,628	11,736
MORGAN	2,993	3,250	4,127	5,629
MOULTRIE	426	1,119	1,060	1,553
OGLE	7,897	9,013	9,337	10,674
PEORIA	1,421	1,564	1,776	2,806
PERRY	8,042	8,275	7,755	9,117
PIATT	875	1,161	1,098	1,709
PIKE	30,886	33,697	34,099	36,886
POPE	9,714	9,232	9,798	10,134
PULASKI	7,827	7,541	7,949	9,452
PUTNAM	292	478	475	868
RANDOLPH	9,061	7,664	7,225	8,944
RICHLAND	4,121	3,134	3,428	5,541
ROCK ISLAND	4,208	4,497	4,678	5,392
ST CLAIR	2,801	2,173	2,311	2,526
SALINE	6,778	6,999	7,808	8,818
SANGAMON	3,991	3,950	4,782	5,803
SCHUYLER	4,428	6,332	6,464	13,146
SCOTT	3,966	3,645	3,098	3,326
SHELBY	8,823	10,166	9,960	12,198
STARK	1,546	1,282	1,176	2,012
STEPHENSON	7,378	7,489	7,147	8,017
TAZEWELL	1,876	3,103	3,278	5,041
UNION	19,091	19,848	19,671	20,310

Table 1. Continued.

COUNTY	Signup 15[a]	Signup 16[b]	Signup 18[c]	Signup 20[d]
VERMILION	2,900	4,280	4,267	5,053
WABASH	2,436	2,501	3,043	3,693
WARREN	1,178	1,348	1,604	1,782
WASHINGTON	6,447	6,262	6,207	6,521
WAYNE	31,710	34,981	39,370	45,213
WHITE	8,888	9,266	9,688	11,478
WHITESIDE	7,583	8,495	9,378	11,744
WILL	1,923	1,504	1,478	1,468
WILLIAMSON	7,851	8,020	8,791	10,938
WINNEBAGO	3,116	3,632	3,871	4,445
WOODFORD	2,470	3,369	3,485	4,998
Total Acreage	605,141	661,537	698,622	838,923

[a]Beginning FY 1998: Accepted plus remaining (acres)
[b]Beginning FY 1999: Accepted plus remaining (acres)
[c]Cumulative acreage as of October 1999
[d]Cumulative acreage as of October 2000

JOB R-1.2: LANDSCAPE/SITE LEVEL BOBWHITE HABITAT

Objective 1: Investigate relationships between bobwhite distribution/abundance and habitat at the landscape and site level.

Identifying factors limiting abundance and distribution of wildlife is essential to understanding their population dynamics. 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, North American Breeding Bird Survey (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 is assumed between the number counted and the number actually in an area. 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 to predict 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. 2002). 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

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Pennsylvania (Klute et al. 2002) and plant species distribution in Florida (Wu and Huffer 1997). Beard et al. (1999) took a similar approach in 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.

Thogmartin (2002) 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 job the influence of environmental parameters were assessed within a spatial linear modeling framework. Given a linear regression model $y = X\beta + e$, 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 of bobwhite presence and abundance were parameterized with NABBS counts. Wildlife managers have used roadside counts of whistling bobwhites such as these as an estimate of relative abundance for >50 yrs (Bennitt 1951, Elder 1956, Rosene 1957, Norton et al. 1961). These count indices indicate relative rather than absolute abundance (Baxter and Wolfe 1972), 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 call count data covered the period 1985-98, a 14-year span which bounds by several years the period in which satellite imagery was taken (1989-92) of the Illinois landscape. The NABBS, 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). 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 1966-98 (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) and greater detail regarding Illinois NABBS call count locations and data are available in Thogmartin (2002).

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 2). 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; the particular script used for these calculations was originally written by Gary Mohr (Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale).

Determining Distribution

Logistic regression was used to assess the influence of environmental parameters on bobwhite distribution. 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).

For any logistic regression, the odds of an event (or no event) given a set of conditions can be determined by calculating:

$$odds = e^{\alpha + \beta 1 x 1 + \beta 2 x 2 + \dots + \beta n x n}.$$

Probability of an event occurring is calculated as: Habitat Suitability Index (HSI) = Probability of Occupation = $odds/(1 + odds)$. Weather parameters from 1977-79 were used to account for the influence of severe winters of the late 1970s on current distribution (Thogmartin 2002).

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, Illinois Department of Natural Resources (IDNR) bobwhite call count sites for 1990, Christmas Bird Count (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

The hypothesis that relative bobwhite abundance varies across sites as the sites vary in their habitat was tested with spatial linear models, accounting for a known correlation between

counts at adjacent survey sites (Thogmartin 2002). Mean abundance ($\log_{10}$-transformed 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 (Thogmartin 2002). 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:

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

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:

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

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. Because it was unclear which suite of variables these authors examined in formulating their final models of presence and abundance, I considered >200 variables in building predictive models of bobwhite presence and abundance. 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.

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

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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. 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, USA) 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 estimated processing 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 (Thogmartin [2002] provided 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.

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Historical effects of the late-1970s winters on current bobwhite distribution were significant (Thogmartin 2002), 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 Thogmartin (2002) and found mean snow days (SNWDY) was highly correlated with elevation ($r = 0.84$). Based on this finding, I re-conducted the analyses substituting elevation with mean SNWDY (Table 2). 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. 1). Unoccupied habitat experienced 36% more days of 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' 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 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. 2). Because of the curvilinear nature of 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. 3).

Model Validation.—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 more 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. 4; log($£$) $= -2,650.6$). Based on this neighborhood of 62, abundance was described as a complex function incorporating polynomials of small grain field shape, sedimentary soil, mean core area of woods, and single variables of the number of woods patches and variability in core area of row crop (Table 3; $AIC_c = 5,062.3$, 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. 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 ($AIC_c = 5,073.3$, $U^2 = 10.9$, $P = 0.0009$). 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 1985-98. 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 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. 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 2002). One goal of avian-habitat relationship studies is to identify environmental conditions controlling presence and abundance of a species. 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

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their Pattern-Recognition Model of Illinois bobwhite habitat; Riitters 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 job 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

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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; 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. L. W. Burger, Jr. (*personal communication*) 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. L. W. Burger, Jr. (*personal communication*) also reported a significant influence of 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[1] 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

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[1]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).

succession due to their high nutrient content, these areas may lack sufficient open ground for bobwhite movement, constraining bobwhite abundance.

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 (Thogmartin 2002).

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), 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) 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) 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).

Potential Bobwhite Population Size in Illinois

Brennan (1999) suggested fall quail densities on high-quality habitat ranged between 2.2 and 4.4 birds $\cdot$ ha^{-1} whereas Leopold (1933) reported bobwhite density rarely exceeded 2.5 birds $\cdot$ 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 $\cdot$ ha^{-1}, 23,527,020 quail at 3.3 birds $\cdot$ ha^{-1}, and 31,369,360 quail at 4.4 birds $\cdot$ ha^{-1}. These estimates are undoubtedly too high. Figure 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 $\cdot$ 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 1/3 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 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 (*Perdix perdix*) have been found to nest in oat fields (Allen 1984) and Warner (1984) reported that ring-necked pheasant (*Phasianus colchicus*) 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[2]. 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 1906-07, not 1956-58. 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 practice in Kansas, indicating the relationship of bobwhite with small grains may be curvilinear. Where this possible apex

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[2] 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.

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.

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.

Table 2. 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)	Unoccupied
Intercept	-12.245	1.269	-9.65	<0.0001		
$\log_{10}(\text{Small Grain}_{5,000\ ha})$	1.822	0.164	11.12	<0.0001	332 ha (10-1,361 ha)	132 ha
$\log_{10}(\text{Shannon's Evenness Index})$	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
$\log_{10}(\text{Woods}_{5,000\ ha})$	0.215	0.126	1.71	<0.0879	906 ha (100-2,817 ha)	746 ha

Table 3. Influence of environmental parameters on relative northern bobwhite abundance in Illinois, as determined by North American Breeding Bird Survey data.

Parameter	β	SE	t	P
Intercept	0.7108	0.0205	34.66	<0.0001
Landscape Shape Index$_{\text{Small Grain, 5,000 ha}}$	0.9013	0.1382	6.52	<0.0001
Landscape Shape Index$^2_{\text{Small Grain, 5,000 ha}}$	-0.4875	0.1032	-4.72	<0.0001
Proportion Sedimentary Soil$_{5,000 \text{ ha}}$	-0.1959	0.0794	-2.47	0.0137
Proportion^2 Sedimentary Soil$_{5,000 \text{ ha}}$	-0.4089	0.0693	-5.90	<0.0001
Row Crop Core Area Coefficient of Variation$_{500 \text{ ha}}$	0.0001	<0.0001	5.24	<0.0001
Number of Woods Patches$_{5 \text{ ha}}$	-0.2750	0.0769	-3.58	0.0004
Mean Core Area/Woods Patch$_{50 \text{ ha}}$	-0.4302	0.0794	-5.42	<0.0001
Mean Core Area/Woods Patch$^2_{50 \text{ ha}}$	-0.1129	0.0648	-3.58	0.08
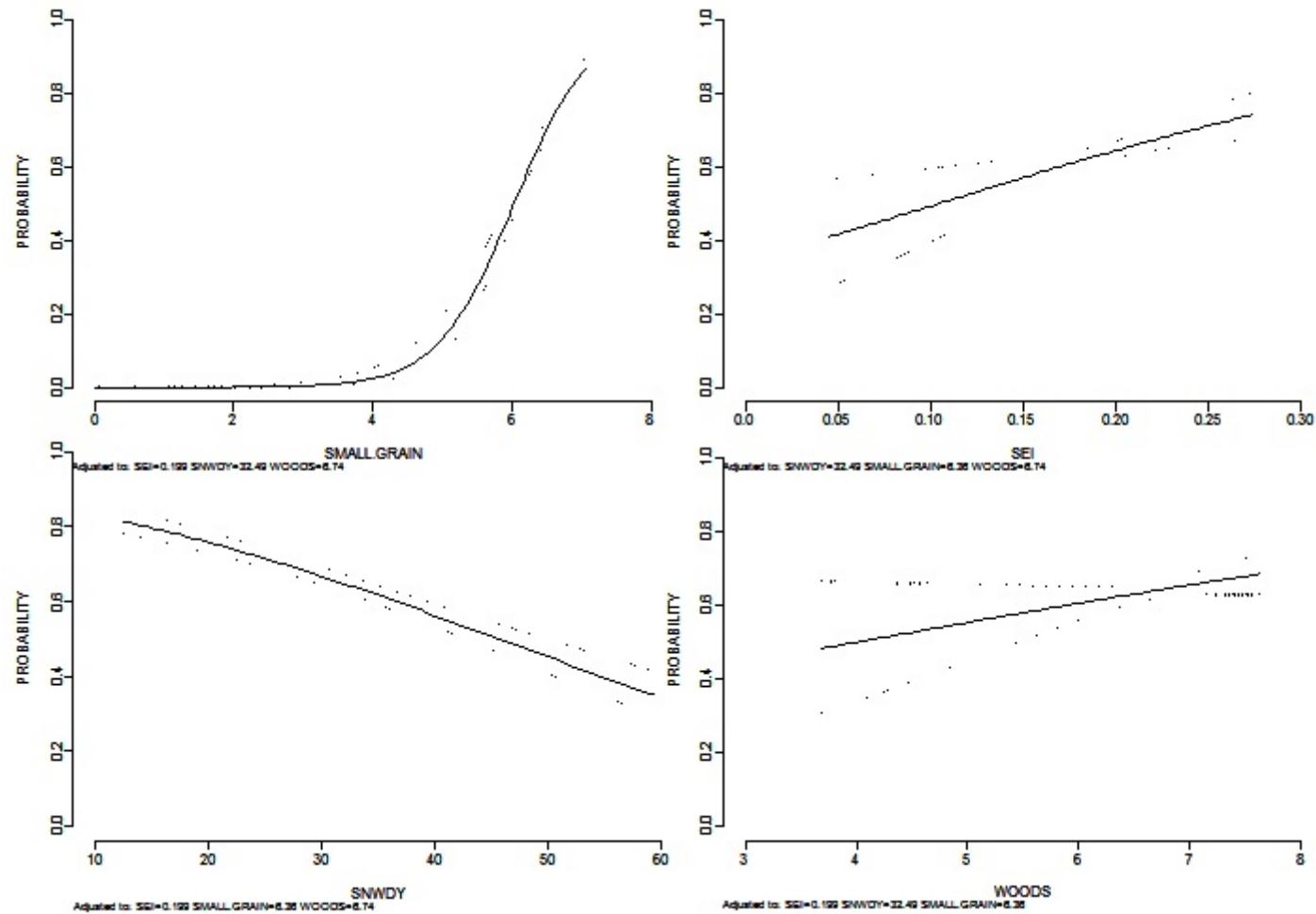
Figure 1. Probability plots, with 95% confidence intervals, for each predictor variable in a logistic regression of northern bobwhite presence in Illinois, 1985-98. SEI is Shannon's Evenness Index, J'.

Lower Confidence Limit   Mean Prediction   Upper Confidence Limit

Habitat Suitability
- 0.50 - 0.55
- 0.55 - 0.60
- 0.60 - 0.65
- 0.65 - 0.70
- 0.70 - 0.75
- 0.75 - 0.80
- 0.80 - 0.85
- 0.85 - 0.90
- 0.90 - 0.95
- 0.95 - 1.00

N
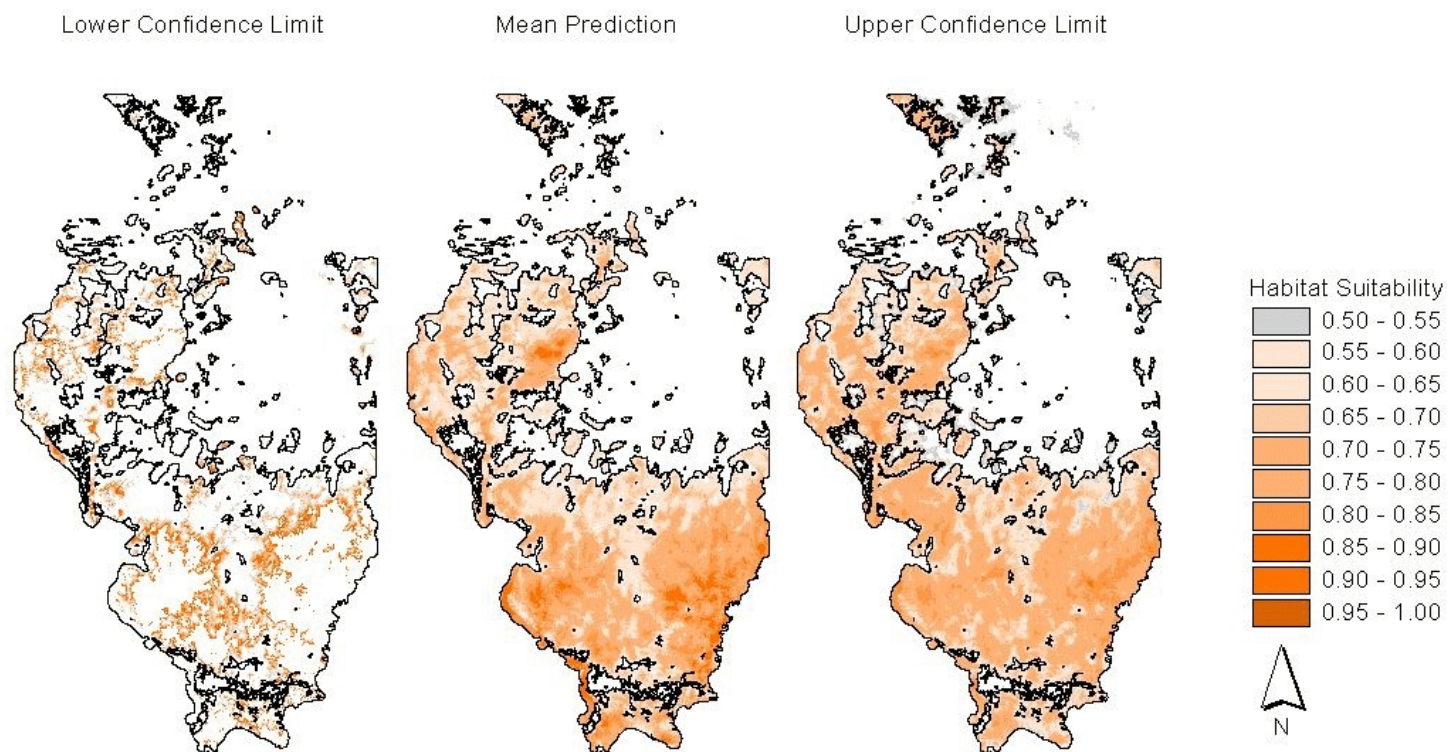
Figure 2. Potentially-occupied landscapes for northern bobwhite (with lower and upper confidence intervals) in Illinois, as derived from North American Breeding Bird Survey data. The outline delineates mean condition in all 3 plots.

HSI = 0.60

HSI = 0.80

HSI = 0.50

HSI = 0.70

HSI = 0.90

Potential Habitat for Northern Bobwhite

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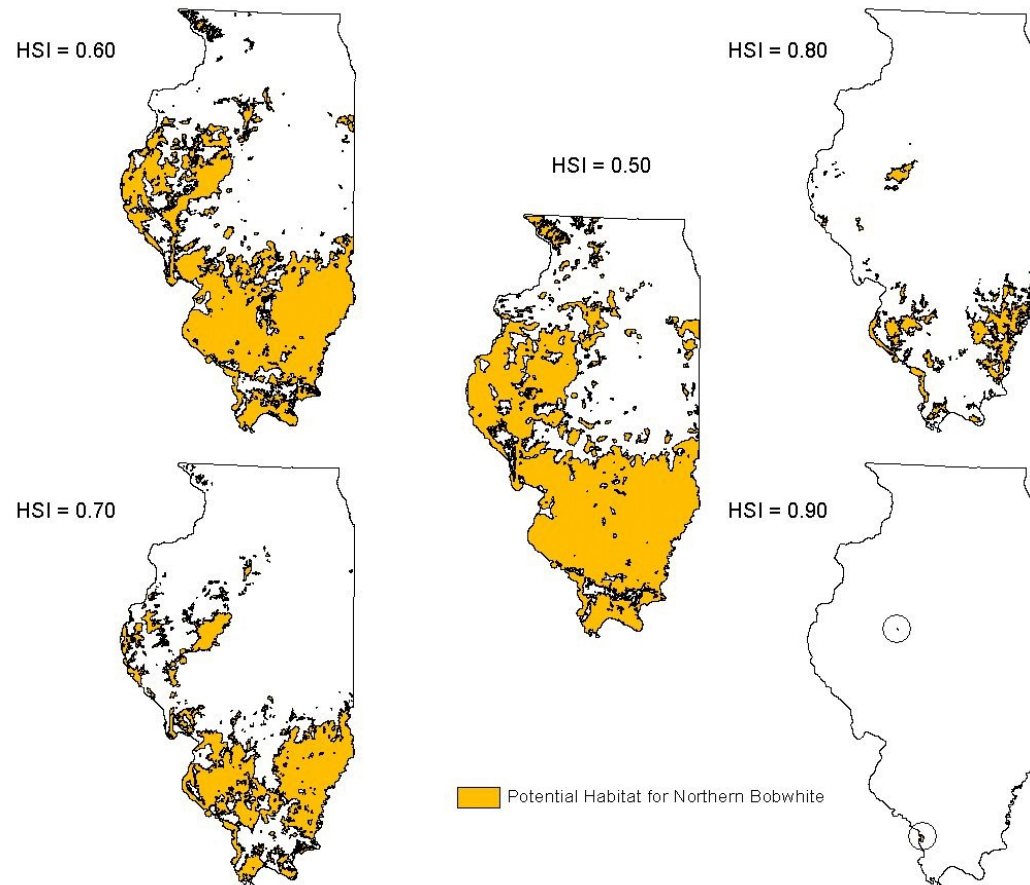
Figure 3. Amount of potentially suitable northern bobwhite habitat in Illinois at various levels of the habitat suitability index, based on the mean model condition. HSI = 0.50 is the mean condition defining lower limit of suitable habitat. Circles highlight habitat at HSI = 0.90.
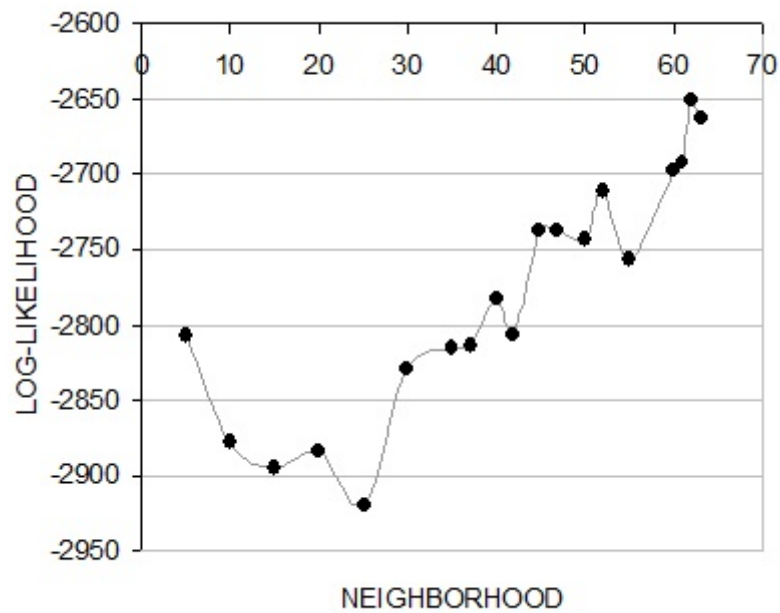
Figure 4. Log-likelihoods for null spatial linear models. The appropriate neighborhood accounting for spatial autocorrelation in bobwhite abundance was the neighborhood (in this case, $n = 62$) resulting in maximization of the log-likelihood.
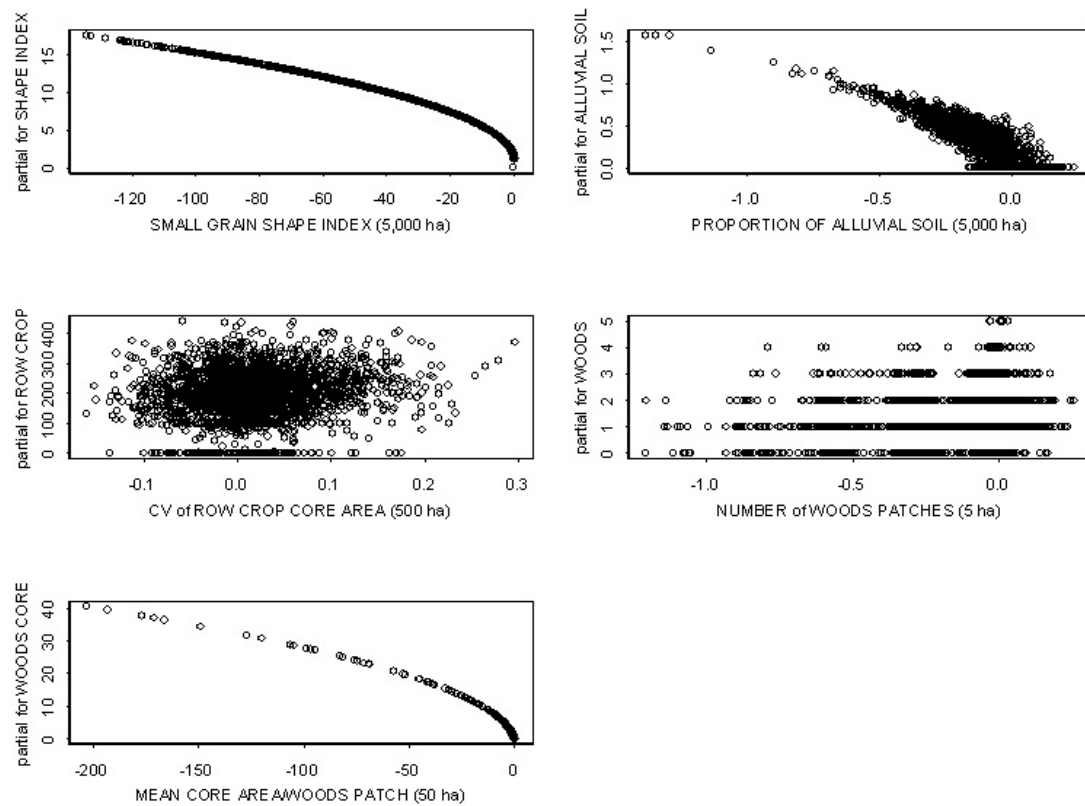
Figure 5. Partial regression plots demonstrating relative influence of environmental variables (see Table 3) on northern bobwhite relative abundance in Illinois, 1985-98.
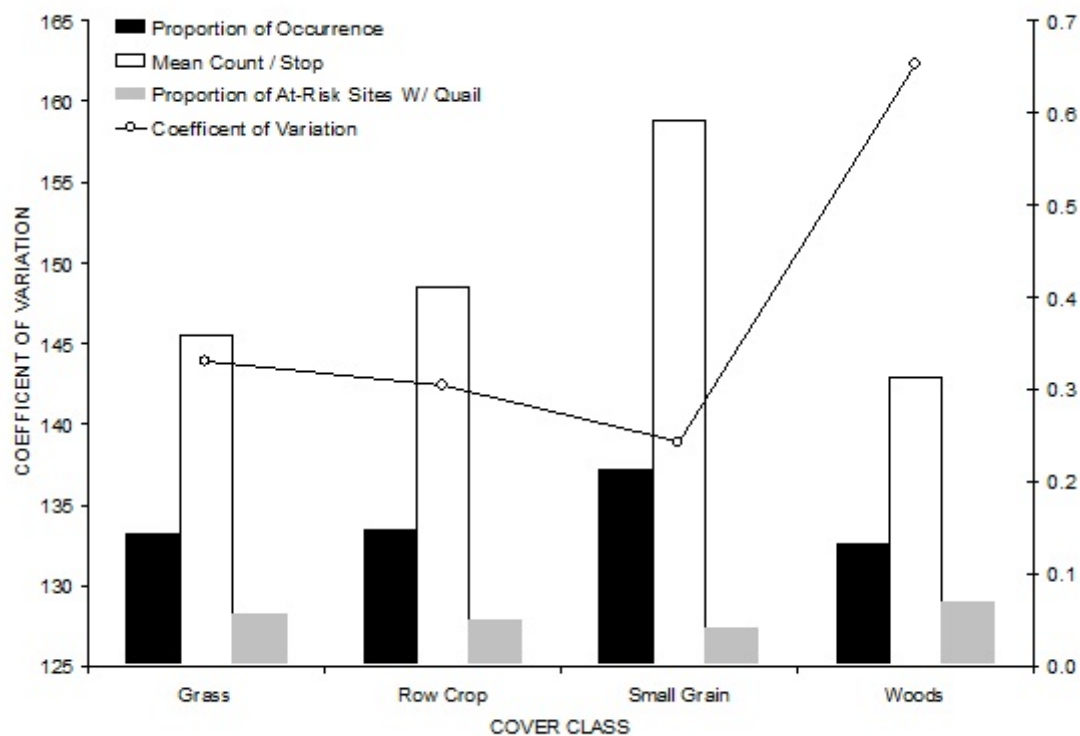
Figure 6. Proportion of occurrence, mean count per stop, proportion of sites with northern bobwhite at risk of extirpation, and coefficient of variation in bobwhite counts by land use/land cover class. Data are from the Illinois portion of the North American Breeding Bird Survey for 1985-98.
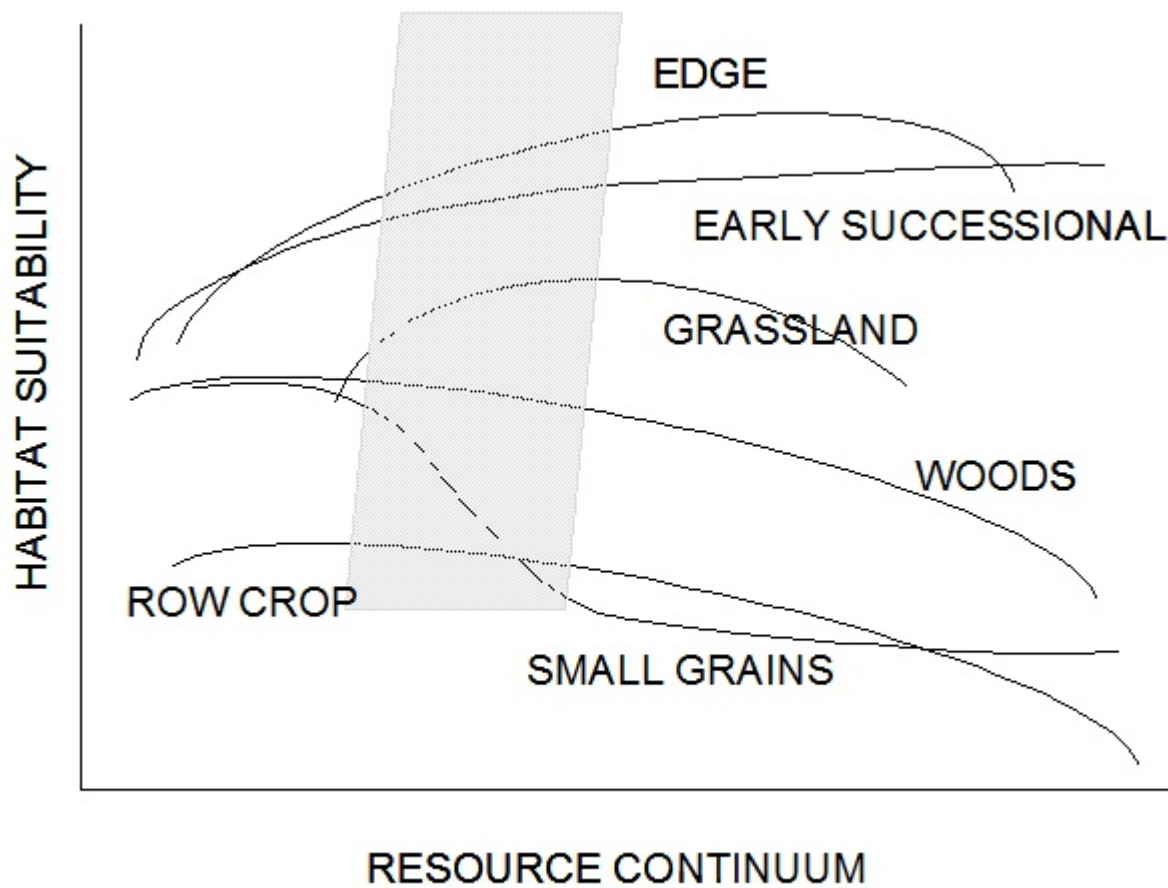
Figure 7. Theoretical relationships of northern bobwhite to various land use/land cover classes. The relative positions, range, and slope of the relationships are currently unknown. The gray parallelogram represents a theoretical optimal configuration of the land cover classes for bobwhite in Illinois.

<u>Objective 2</u>: Identify limiting components in unoccupied or sparsely populated areas and evaluate the feasibility of restoring them.

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 (1994a,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 precluded use of this method because patterns of individual patch occupancy were unknown. However, I did have information regarding patterns in population extirpation and recolonization (Thogmartin 2002). Sjögren-Gulve and Ray (1996) outlined a procedure whereby it is possible to model metapopulation dynamics with information regarding population state transitions. I used this 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 and thus reveal factors limiting occupation in areas where bobwhite were absent or only sparsely abundant. The questions I asked were: what habitat variables govern population-state transitions? Do empirical data indicate a metapopulation approach is valid for management purposes?

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 one such alternative (Wolf et al. 1996). I prioritized previously identified quail population networks for management action, with the prioritization focusing on identifying habitat suitable for recolonization.

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 (Thogmartin 2002). 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 ArcGIS 8.0 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 identified, 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; Illinois, Bartholomew 1967; Iowa, Crim and Seitz 1972; Illinois, Urban 1972; Tennessee, Yoho and Dimmick 1972).

Modeling Patch-State Transitions

Logistic regression was used to relate environmental variables to a dichotomous response. 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 IDNR call counts because they offered a robust measure of turnover probability (Thogmartin 2002).

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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. 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 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. 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 used to predict

Capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*) 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 derived from a review of the literature (Table 4) were altered to reflect the slight downward trend in abundance observed since 1981 (Thogmartin 2002).

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 1971). 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).

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.

Prioritizing Populations for Translocation

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 Thogmartin (2002). I assessed various

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weightings of each criteria to determine the sensitivity of rankings to changing emphasis, but found that rankings varied little. I concluded with only a simple ranking based upon the sum of equally-weighted ranks across the 5 criteria.

RESULTS

Dispersal Probability Function

Fifteen studies reported movement distances (Table 5); 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). From Sutherland et al.'s (2000) equations, bobwhite in Illinois were hypothesized to disperse a median distance of 1.5 km (range = 0.34–2.07 km) and a maximum distance of 35.3 km.

State-Transitions

Calculation of Somers' D (Table 6) 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 adequately (C > 0.70) described 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 7). 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

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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 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). 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). 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 Human$_{500\ ha}$ with CLAND$_{Woods,\ 50\ ha}$. 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

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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.

Population Structure

An ArcView shapefile created from the limiting habitat grid layer revealed 416 patches of habitat >4 ha occurring in 52 networks (Fig. 9). 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 $\geq$1,000 ha ($n = 56$) comprised 647,409 ha, or 8% of potential habitat (Fig. 10a).

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). Only when contours of 2 km were established were significant numbers of patches isolated from one another. In general, population networks possessed $\leq$5 patches (Fig. 10b). 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 9, $F_{2, 44} = 1,367$, $R^2 = 0.98$, $P < 0.0001$), indicating larger initial populations lasted longer. Number of neighbors in a metapopulation contributed a small, but significant, positive amount to the explained variance.

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 MCA2$_{\text{Grass, 5,000 ha}}$ and IJI$_{\text{Small Grains, 5,000 ha}}$. One model contained MCAI$_{\text{5,000 ha}}$ and Human$_{\text{500 ha}}$, whereas the other contained CLAND$_{\text{Woods, 50 ha}}$. 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

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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 a 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 (Thogmartin 2002). 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.

Another 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 persistence. The U.S. Department of Agriculture Natural Resources Conservation Service indicated >6.5 million ha 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 (Thogmartin 2002).

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 (Thogmartin 2002). 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 (Thogmartin 2002). 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

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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.

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.

Prioritizing Populations for Translocation

One-hundred-seventy-one patches (1,944 km^2) were predicted to be either unoccupied or sparsely occupied (Fig. 11). Mean landscape suitability in these patches was 0.517 ± 0.001, below the lowest observed occupied habitat suitability index value (Thogmartin 2002). 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. 12). 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.

Table 4. 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
$\bar{x}_{dispersal}$ 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

Table 5. 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)

Table 6. 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 7. 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	
$\text{TCAI}_{5,000 \text{ ha}}$	0.035	0.006	5.66	<0.0001	1.036 (1.023-1.048)
$\text{MCAI}_{\text{Woods, 5,000 ha}}$	0.060	0.026	2.30	0.0214	1.061 (1.009-1.116)
$\log(\text{MNN}_{\text{Row Crops, 5,000 ha}}+1)$	1.661	0.566	2.94	0.0033	5.264 (1.737-15.950)
$\log(\text{Woods Area}_{50 \text{ ha}}+1)$	0.536	0.159	3.36	0.0008	1.709 (1.250-2.335)
$\log(\text{MPI}_{50 \text{ ha}}+1)$	0.385	0.228	1.69	0.0907	1.469 (0.941-2.295)

Table 8. 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	
$MCA2_{Grass,\ 5,000\ ha}$	1.582	0.358	4.42	<0.0001	4.867 (2.412-9.820)
$IJI_{Small\ Grains,\ 5,000\ ha}$	0.017	0.007	2.48	0.0132	1.017 (1.004-1.031)
$MCAI_{5,000\ ha}$	0.561	0.336	1.67	0.0944	1.753 (0.908-3.385)
$Human_{500\ ha}$	11.058	4.506	2.45	0.0141	63,475 (9.3->4 million)
Intercept[b]	-2.142	0.428	-5.00	<0.0001	
$MCA2_{Grass,\ 5,000\ ha}$	1.708	0.348	4.90	<0.0001	5.519 (2.789-10.924)
$IJI_{Small\ Grains,\ 5,000\ ha}$	0.019	0.007	2.79	0.0053	1.019 (1.006-1.033)
$CLAND_{Woods,\ 50\ ha}$	1.638	0.548	2.99	0.0028	5.142 (1.758-15.039)

[a]Model 1
[b]Model 2

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Table 9. 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	5,770.2
Neighbors	0.17	0.08	2.19	0.0338	10.2
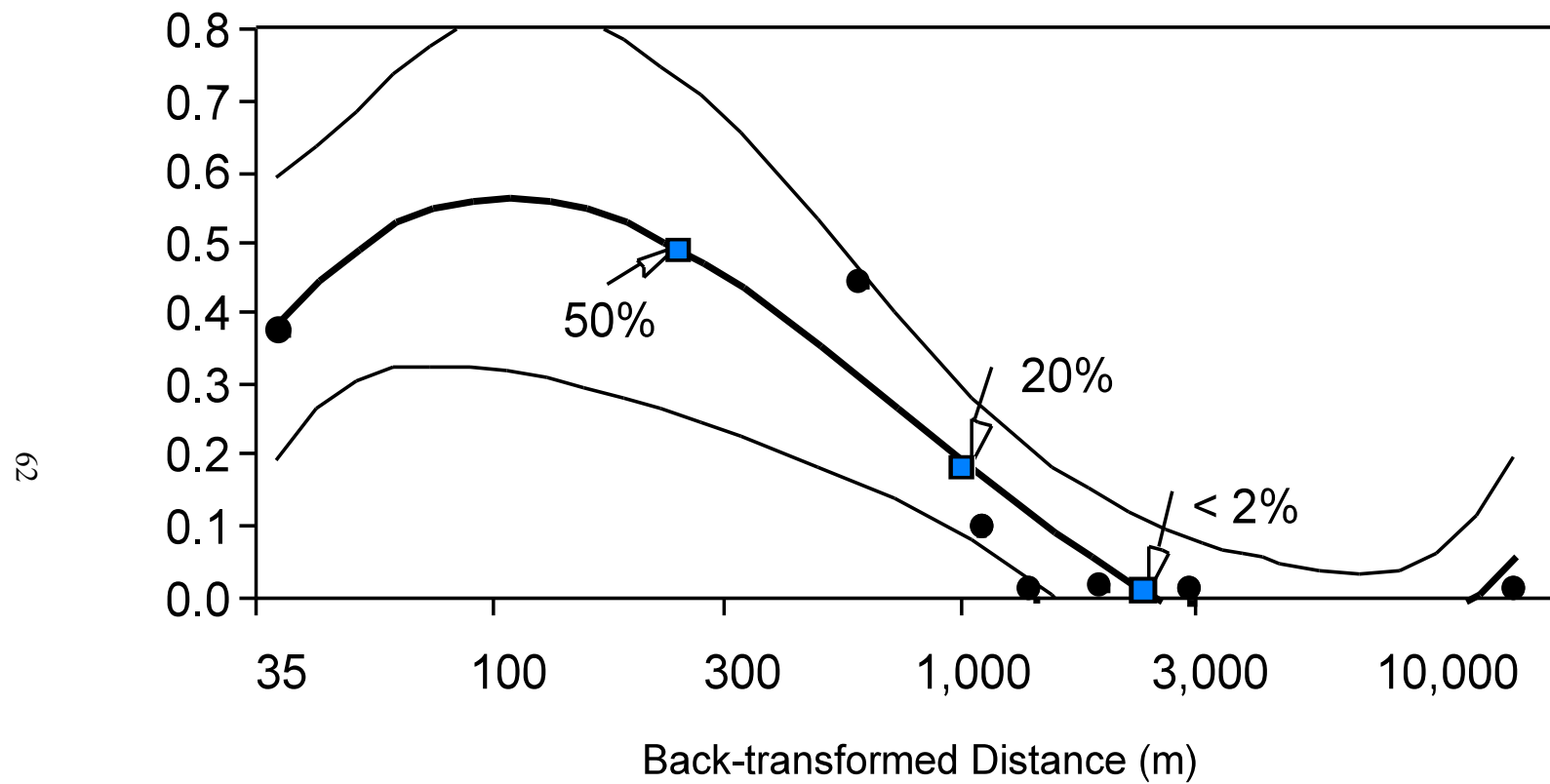
Figure 8. Dispersal probability function derived from reported bobwhite dispersal movements. The black line is a polynomial (95% CI) fitted to the observed values.
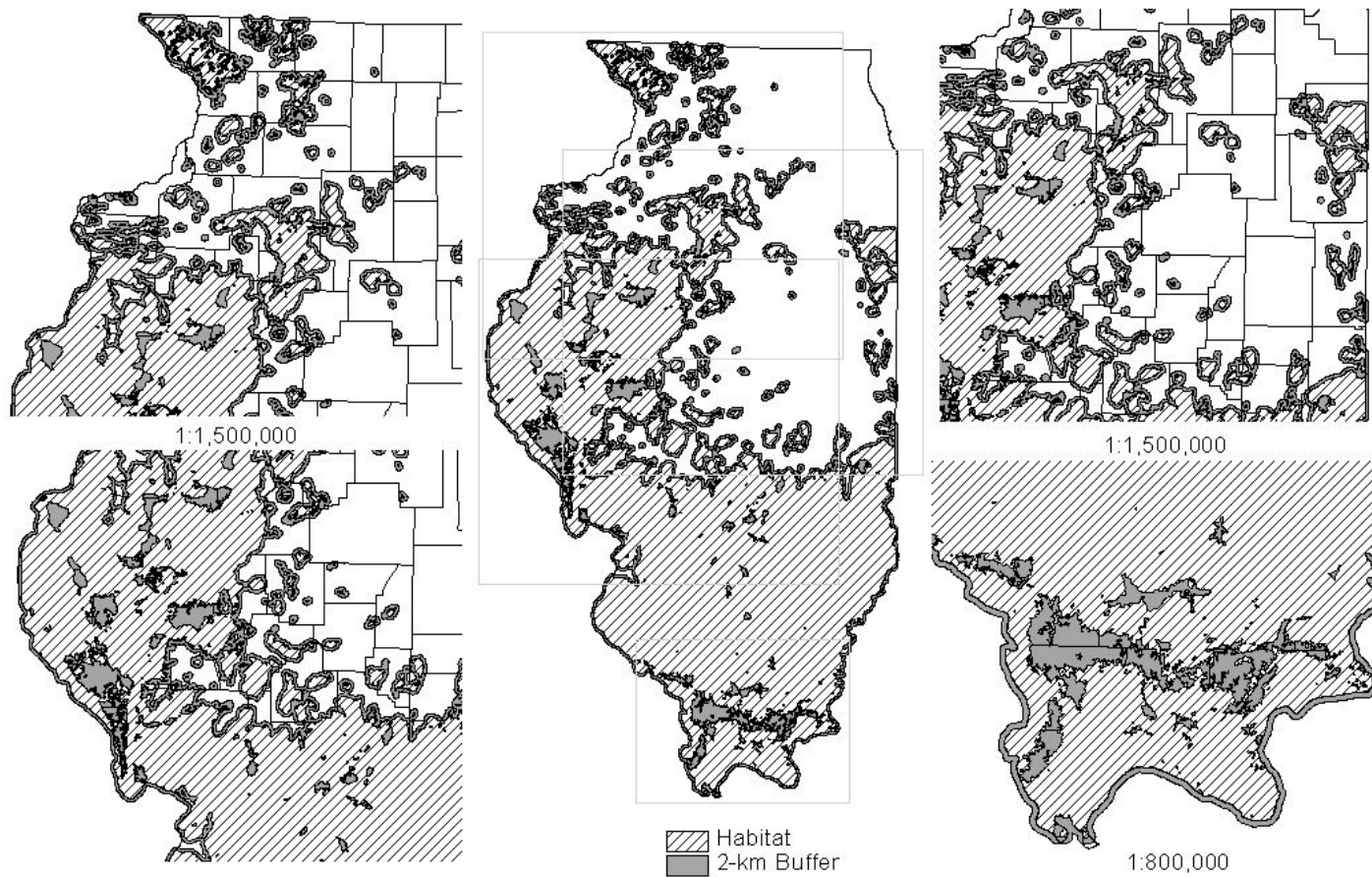
Figure 9. Potentially suitable northern bobwhite habitat in Illinois delineated into unique metapopulations by a 2-km buffer representing the typical maximum dispersal distance of the species.

A
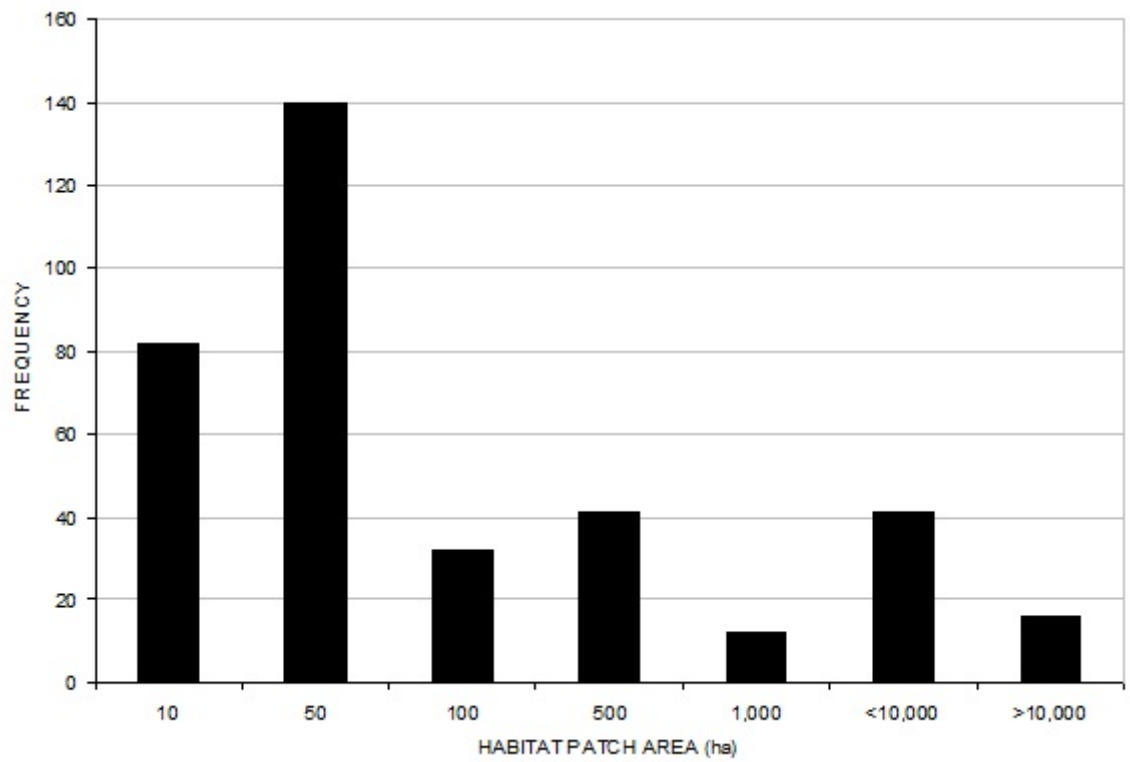
B
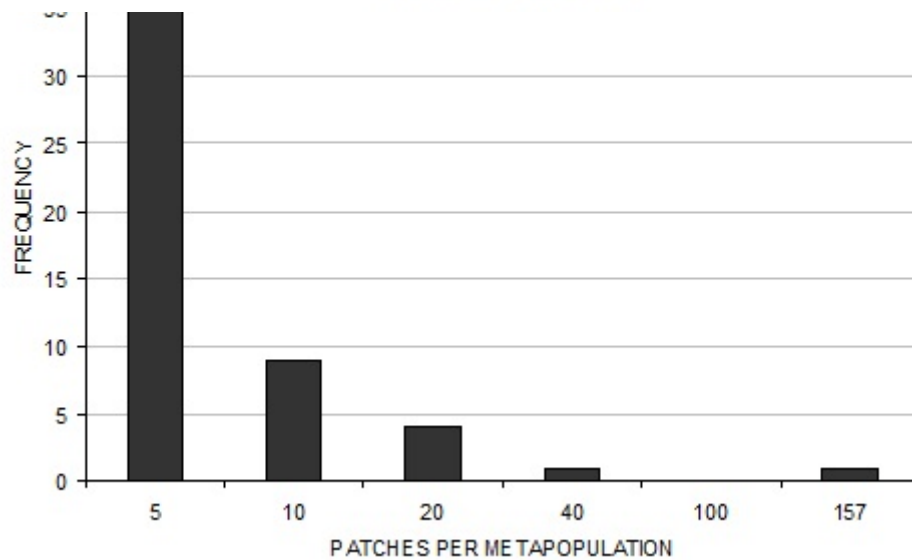
Figure 10. A) Frequency distribution of suitable habitat patch sizes and B) patches per metapopulation for northern bobwhite in Illinois, as determined from a model of landscape-level habitat suitability.
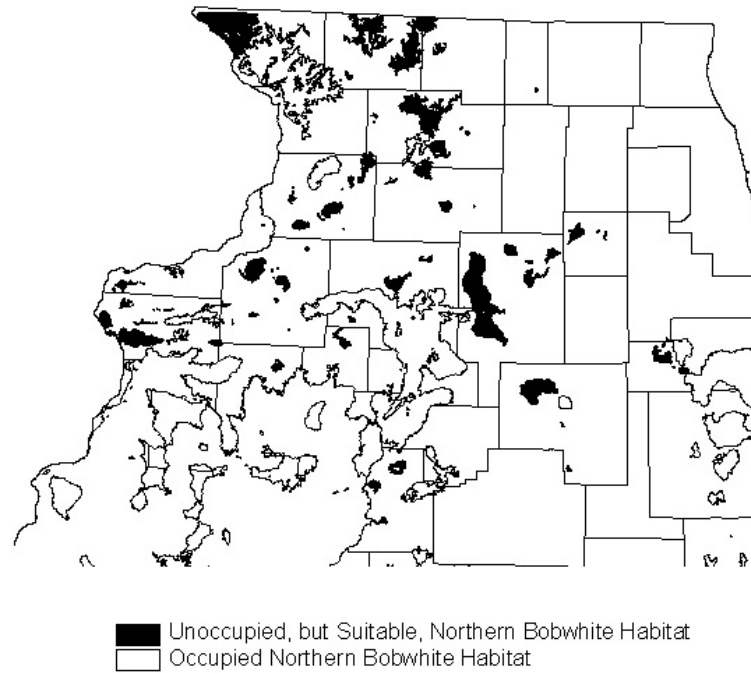
Figure 11. Suitable northern bobwhite habitat in Illinois predicted to be unoccupied or sparsely populated (in black) based on effects of historical winter weather of the late-1970s.
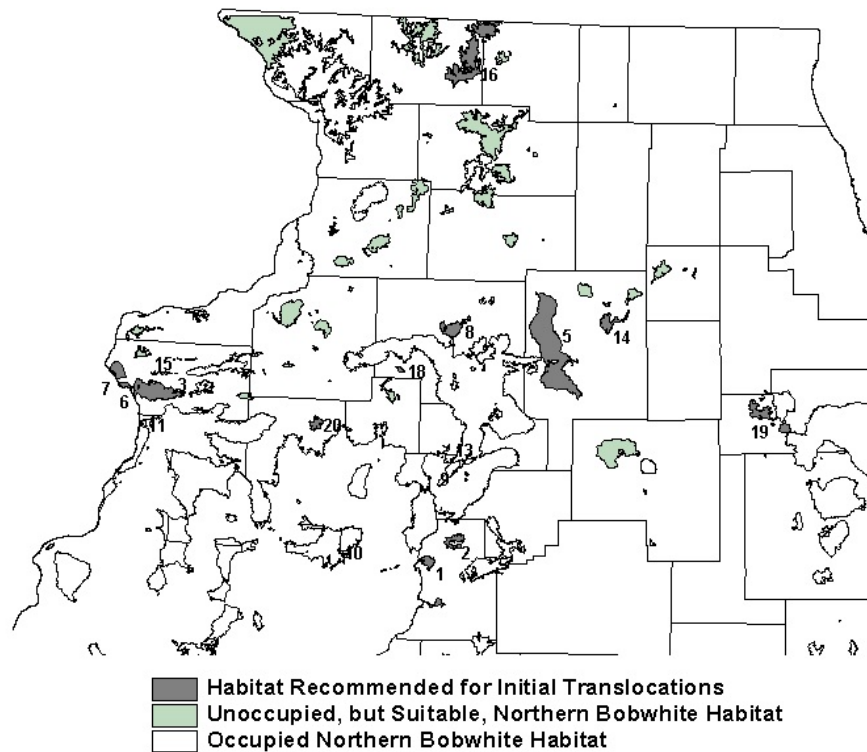
Figure 12. Habitat most suitable for translocation of northern bobwhite. The top 20 choices are numbered and are a darker gray.

<u>Objective 3</u>: Examine relationships between population parameters, observed population
decline, and seasonal climatological conditions.

For the past 50 years, wings from bobwhite have been submitted by southern Illinois
hunters to monitor sex- and age-structure of Illinois quail. This wing collection represents the
longest running monitoring effort for bobwhite, and one of the longest for all wildlife species.
Over this same period, bobwhite have experienced an unprecedented decline in abundance
(Brennan 1991); for instance, analyses of NABBS (Droege and Sauer 1990, Church et al. 1993)
and CBC (Brennan 1991) data indicated bobwhite have declined in 77% of the states in their
range since the late-1960s. This decline was approximately $2.8\% \cdot yr^{-1}$ in Illinois since 1966
(Sauer et al. 2000), primarily because of intensified agricultural land use (Klimstra 1982,
Brennan 1991).

Future predictions of population abundance in response to intrinsic and extrinsic factors
will be aided by discerning functional relationships between environmental parameters and
subsequent biological responses. We used these wing-derived data to examine potential
relationships between age- and sex-structure and temporal patterns in abundance. Our first
concern was whether biological response parameters derived from wing data corresponded with
surveys of relative abundance (e.g., NABBS) collected at various times of the year. We also
discerned relationships between biological response parameters (intrinsic factors), and
climatological information and historical state agriculture data (extrinsic factors). There is
extensive documentation of the effects of weather on bobwhite (e.g., Roseberry 1962, 1989;
Roseberry et al. 1979; Thogmartin 2002), and because >80% of Illinois' 14.4 million hectares is
currently farmed (Illinois State Geological Survey 1994), we hypothesized significant changes in
bobwhite biological response over time would be due to changes in these 2 factors.

METHODS

We annually collected bobwhite wings from hunters in the 34 southernmost counties of
Illinois between 1950 and 2001 along with information relating to location, sex, and date of

harvest. Age of each bird was determined by feather replacement and molt pattern (Leopold 1939, Petrides and Nestler 1952). From the age of individual birds we derived the ratio of juveniles per adult (JPA), a commonly used index of productivity in this species (Roseberry and Klimstra 1984). Within adult and juvenile age classes, we derived the ratio of males to females (MA and MJ, respectively). We determined the number of adult females in the previous year surviving to the year of harvest (PREFAD); since nearly 100% of female bobwhite reproduce each year (Brennan 1999), this metric indexes the proportion of experienced female breeders in the population. Based on age and date of harvest, we determined the proportion of juveniles hatched after 29 July (H29) and 12 August (H12). We determined the number of birds killed per hunter trip (KILL) from hunter questionnaires and calculated an annual percent change in kill per trip (CKILL). Because effects in a parameter in any 1 year may not be evident until future years, we also created 4 lagged parameters, offsetting JPA, MA, MJ, and KILL by 1 year (PREJPA, PREMA, PREMJ, and PKILL, respectively). These metrics of population response were used as dependent variables in our statistical models. To differentiate long-term trends from annual variation in parameters we applied a locally-weighted regression (loess) which applies a nonparametric smooth response surface model to the annual estimates. The fit of this model described the long-term trend in the biological response parameter; residuals from the fit described annual variation about the long-term trend.

Daily and seasonal historical climate data were collected from 28 southern Illinois weather stations (U.S. Department of Commerce 1950-2001). Data were then combined for each month and biological season (Table 10). These data included mean, minimum, and maximum temperature, mean precipitation, number of days in winter with snow ≥ 2.54 cm, Thornthwaite's index of potential evapotranspiration (Thornthwaite 1948), and modified Palmer drought severity index (Palmer 1965, Bridges et al. 2001). Thornthwaite's index of evapotranspiration integrates maximum daily temperature, soil moisture, and precipitation into a measure accounting for moisture gains, losses, and the consequent changes in water storage occurring over successive

time periods. The modified Palmer drought severity index (MPDSI) is based on precipitation and temperature data, as well as local available water content of the soil (Alley 1984, Heddinghaus and Sabol 1991). Annual agricultural data included number of farms, farm size, area devoted to corn, winter wheat, oats, sorghum, barley, and rye, and several measures of cattle production (National Agriculture Statistics Service, http://www.nass.usda.gov:81/ipedb/). An estimate of agricultural grassland was derived by differencing hectares of corn and soybean from the total hectares in agricultural production.

We used non-parametric correlation to relate annual indices of biological response to estimates of relative bobwhite abundance as derived from the NABBS (1967-98), Illinois Department of Natural Resources bobwhite call count surveys and harvest data (1975-98), and CBC surveys (1967-98). Temporal autocorrelation in response parameters was assessed with autocorrelation and partial autocorrelation function plots. Both linear models and autoregressive models (i.e., models incorporating potential temporal autocorrelation) were evaluated, with the final suite of models used for inference determined by Aikike's Information Criterion (Aikike 1973, Burnham and Anderson 2000). Only models performing better than the null model are reported.

RESULTS

A total of 183,264 wings was examined between 1950 and 2001, annually averaging 3,524 wings (range = 1,332–5,913). The mean ratio of juveniles to adults was 4.93 (SD = 1.13), and ranged from 2.39 to 8.42 (Fig. 13, Table 11). Indices of abundance were most consistently related to JPA, KILL, and PKILL (Table 12). Higher abundance was related to a lowered ratio of juveniles to adults, whereas kill/effort was positively related to abundance, at least after 1967.

The number of juveniles per adult fluctuated considerably over the period of study (Fig. 13). However, within this interannual fluctuation, mean JPA declined across the period 1950 to 1970; thereafter mean JPA was stationary. This long-term trend in JPA was associated with amount of land devoted to agricultural grassland in Illinois (Table 13; adj-R^2 = 0.892, $F_{1,49}$ =

406.2, $P < 0.0001$). Annual variation in JPA was associated with precipitation during hatching, temperatures in winter, and the previous year's harvest (Table 14; adj-$R^2 = 0.518$, $F_{3,37} = 13.27$, $P < 0.0001$).

The proportion of adult males in the adult age group (MA) consistently exceeded 55%, and in only 1 year, 1957, was the proportion of adult males <53% (Fig. 14). The proportion of males in the juvenile age group (MJ) did not differ from 50% (95% CI: 49.9-50.8). It should be noted that when MA was <50% in 1957, production by bobwhite, as measured by JPA, was the second highest (7.26 juveniles·adult^{-1}) observed over the 50-yr period; this appears to be an anomaly, however, as this pattern was not repeated when JPA again peaked in 1980. Neither MA nor MJ indicated the presence of a long-term trend; therefore, only annual variation in the actual time series was examined. Visual inspection of MJ plotted over time suggested the possibility of serial correlation within the time series, but neither a runs test ($t_s = -0.9$, $P > 0.05$) nor a plot of the autocorrelation function indicated the presence of significant serial correlation. As noted previously by Roseberry and Klimstra (1984), there was a weak but significant tendency ($r = -0.32$) for MJ to be slightly higher during years of population decline; MA showed no such relationship. Neither annual variation in MA and MJ nor the variables themselves were associated with the environmental covariates we examined. MA was only slightly correlated with MJ the previous year, ($r = 0.19$). If environment rather than simple random variation influences within-age group sex ratios, then we likely were precluded from elucidating environmental influences on MA and MJ because of very little year-to-year variation around the mean condition (CVs < 7.2%) and coarseness of the explanatory variables we examined.

Mean percent of bobwhite hatched after 29 July (H29) was 27.6% (range = 13.6-40.6%) (Fig. 15); mean percent of bobwhite hatched after 12 August (H12) was 8.2% (range = 3.9-28.7%). Both H29 and H12 led to similar models, so we report only those for H29, the earlier estimate of proportion hatched. The long-term trend in H29 was a curvilinear function of annual hay production (Table 13; adj-$R^2 = 0.952$, $F_{2,45} = 465.4$, $P < 0.0001$). A weaker model indicated

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the long-term trend in H29 was a curvilinear function of agricultural grassland (Table 13; adj-R^2 = 0.906, $F_{2,46}$ = 225.5, $P < 0.0001$). Though each parameter explained nearly all of the long-term variation in the proportion of late-hatch juveniles, based on the difference in Aikike's Information Criterion, the most parsimonious explanation included only hay production (ΔAIC = 92). Limiting explanatory variables to those derived for late winter, spring, and summer (i.e., excluding autumn weather variables) led to models of annual variation in H29 performing little better than the null model (Table 15). The best performing model combined elements of August and January evapotranspiration (Table 14; adj-R^2 = 0.171, $F_{2,47}$ = 4.9, $P = 0.012$).

Since 1960, the number of birds killed per trip varied between 2.33 and 4.94, with a mean of 3.57 (Fig. 16), whereas the annual percent change in birds killed per trip varied between -33 and +50%. The long-term trend in KILL was closely associated with a decline in agricultural grassland and changes in precipitation during the hatching period (10 June through August) (Table 13; adj-R^2 = 0.930, $F_{3,46}$ = 215.6, $P < 0.0001$). Models with hay and oats instead of total grassland were >30 AIC units removed. Annual variation in KILL was associated with a complex function of KILL in the previous year, number of days of snow >2.54 cm, minimum temperature in June, mean temperature in July, and evapotranspiration in August and November (Table 14; adj-R^2 = 0.431, $F_{6,33}$ = 4.2, $P = 0.003$). Models dropping evapotranspiration in November and another also deleting evapotranspiration in August were similarly weighted as the full model ($\Delta AICs < 2.4$); thus, inference can be made on the smaller model or on the entire suite of nested models. No models for CKILL performed better than the null model.

DISCUSSION

Annual Variation

Juvenile Per Adult Ratio.— JPA is a complex index of production integrating 10 demographic variables (Guthery and Kuvlesky 1998). These demographic parameters are (1) proportion of females in the breeding population, (2) proportion of females participating in reproduction, (3) potential number of nesting attempts per individual female, (4) probability of

nesting success for any individual attempt, (5) number of eggs hatching, (6) daily juvenile survival rate, (7) daily adult survival rate, (8) length of the laying period, (9) time committed to laying and incubation, and (10) the proportional distribution of successful breeding starts per hen in time (Guthery and Kuvlesky 1998:540-541). As Guthery et al. (2002) suggested, there are many combinations of these demographic parameters leading to the same age ratio. For instance, high JPA can actually reflect high production, as we observed for 1957, or it may reflect high summer losses (e.g., possibly the late-1970s), variation in chick survival, or simply a density-dependent response to low breeding populations (e.g., late-1970s). Thus, high JPA may be correlated with both high and low autumn populations. Correlation between JPA and KILL over the 40-year study period was negligible despite a negative correlation of JPA and abundance data since 1967; there was, however, a positive correlation ($r = 0.42$) between JPA and CKILL, the percent change in kill from 1 year to the next, agreeing with Roseberry (1974).

Guthery et al. (2002) modeled the relationship between a 35-year, intermittent time series of JPA and climatological parameters in south Texas and found age ratios increased with June temperature and seasonal precipitation, most notably that occurring in spring; August temperature and temperature in July below 36 °C did not influence JPA. We found for Illinois populations of bobwhite that annual variation in JPA was attributed to precipitation during hatching (Jun to Aug, i.e., summer), temperatures the previous winter, and the previous year's kill per trip. High precipitation during hatching has been shown to increase chick mortality (Baker and Robinson 1952, Speake and Haugen 1960, Stanford 1972) and cold winter conditions reduce recruitment of breeders into the subsequent spring (Roseberry and Klimstra 1972, Stanford 1972). However, the most parsimonious model possessed coefficients opposite of the expected direction (Fig. 17); greater precipitation during the hatching period was associated with an increase in the ratio of juveniles to adults, whereas increased winter temperature and kill per trip in the previous year were related to a reduction in this ratio. Decreases dues to increasing winter temperature and kill per trip may reflect density-dependent responses by bobwhite to

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favorable conditions. The negative effects on chick survival by increased precipitation during the hatch may be outweighed by the positive benefits precipitation has on vegetative growth and insect production.

In south Texas, where rainfall is limiting, timing and amount of precipitation may explain >70% of the variation in bobwhite abundance (Rice et al. 1993), where, for instance, <10 cm of rainfall results in ≤3 juveniles per adult. However, drought is only rarely associated with variation in bobwhite abundance in the midwestern U.S. (Roseberry 1989). Thus, if this model correctly explains bobwhite JPA, lower bounds apparently exist in summer precipitation in the Midwest which influence bobwhite productivity. Effects of the long-term trend in JPA may have obfuscated these effects previously.

Proportion of Late-hatched Juveniles.—Similar to JPA, the late hatch indices H29 and H12 may reflect variation in nest success relative to some combination of timing of nest initiation, termination of nesting, and extent of renesting. Thus, these late-hatch indices may be related to spring conditions, summer conditions, or, possibly, neither. After excluding autumn weather variables, which should have no effect on hatch chronology, we were unable to infer strong relationships between climate and annual variability in the proportion of late-hatched juveniles; we derived marginal relationships of potential evapotranspiration in January and August to H29. Higher evapotranspiration, which is a dynamic combination of temperature, soil moisture, and humidity, was associated with a lower proportion of chicks hatched after 29 July, probably because conditions earlier in the year were conducive to earlier initiation of nesting season; warmer, wetter Januaries likely led to earlier green-up. Conversely, high evapotranspiration in August was likely associated with the termination of nesting activity.

Theoretically, a high proportion of late-hatched juveniles could be positive if it represented multiple brood production by individual hens, or negative if it reflected poor success of initial nesting attempts. Our data suggest the latter is more likely. Over the entire range of data, H29 demonstrated a modest negative correlation ($r = -0.37$) with KILL. Since 1967, a

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higher percentage of late-hatched also was associated with lower IDNR harvest estimates ($r = -0.43$).

Long-term Trends

Juvenile Per Adult Ratio.—The decline in mean JPA from 5.8 in the 1950s to 4.4 between 1967 and 1972 was 24%; assuming equal survivorship between periods, this is equivalent to a decline in clutch size from 14 to 11 eggs·clutch^{-1}. We associated this long-term trend in the number of juveniles per adult with amount of farmed land devoted to herbaceous grassland. What we defined as agricultural grassland consisted of all lands devoted to pasture, hay, small grains (i.e., winter wheat), fallowed cropland, set aside, and grain sorghum. The bias associated with including sorghum, a row crop, in our estimate of agricultural grassland was small given annual production never exceeded 106,000 ha. Agricultural grasslands may act as an ecological surrogate to native prairie, given that remnant prairie is <0.01% of its former occurrence (Taft 1995). Thogmartin (2002) found significant associations between land in Illinois devoted to small grain production and bobwhite presence, abundance, and population extirpation; grassland, too, influenced bobwhite population extirpation probability.

Proportion of Late-hatched Juveniles.—The proportion of juveniles hatched late in the summer (H29 and H12) increased throughout the 1950s, 1960s, and early 1970s, peaking in the mid-1970s. Thereafter, the proportion of late-hatched juveniles declined to some extent, especially for the hatch after 12 August. Given the high correlation between the long-term trend in JPA and proportion of late-hatched juveniles ($r_{JPA,H29} = 0.94$) it is not surprising that the proportion of late-hatched juveniles was also associated with the amount of herbaceous grassland in production. However, a component of agricultural grassland, hay production, actually fit the data better, as 95% of the variation in hatch matched temporal patterns in amount of the Illinois landscape devoted to haying. Over this 50-year period, agricultural grasslands have declined tremendously in central and southern Illinois, though the proportion devoted to hay production has concomitantly increased (J. Cole, Illinois Department of Natural Resources, *unpublished*

report). In the Kaskaskia Watershed, for instance, the percentage of agricultural grasslands devoted to hay increased from 21% in the 1960s to 32% in the late 1990s whilst the proportion of agricultural grassland in the landscape declined from 16% to 7% in this same period. Concurrently, changes in species composition and management activities in hay and pasture lands have occurred as well, moving from diverse assemblages of grasses and forbs to monocultures of tall fescue (*Festuca arundinacea*) and alfalfa (*Medicago sativa*).

The gradual change in both number of juveniles per adult and the proportion of juveniles hatched late in summer may signal the degradation, rather than absolute loss, of bobwhite habitat in the 1950s, 1960s, and early 1970s. We offer this hypothesis based on the following rationale. Over the course of the 50-year study, hunter numbers in Illinois have plummeted whilst the age of bobwhite hunters (and, thus, their experience) has increased (Burger et al. 1999, Enck et al. 2000). Undoubtedly, some hunters were lost due to the loss of suitable habitat for hunting. However, if the increasingly experienced, remaining hunters hunted land less affected by habitat degradation then we should not expect to see changes in the measures of biological response available from hunter-contributed wings. This is because climate parameters contributed little to explaining long-term trends in response parameters as opposed to land use parameters.

The means by which bobwhite habitat may have degraded, leading to the observed patterns in hatch proportion and juveniles produced per adult, are offered by Riley and Riley (1999) for ring-necked pheasant (*Phasianus colchicus*). They attributed lowering of pheasant brood size over time to gradual reductions in the availability of suitable nesting and brood-rearing habitat, causing increased loss of initial nesting and brooding attempts (T. Z. Riley, Director of Conservation, Wildlife Management Institute, *personal communication*). Clutch sizes of initial nests by bobwhites maybe >20% larger than subsequent nesting attempts (Roseberry and Klimstra 1984). Thus, if initial nesting success declines relative to subsequent renests, then the proportion of juveniles hatched later in the summer will necessarily increase. Unfortunately, there are little data to confirm this supposition for bobwhite in Illinois. Results in

Roseberry and Klimstra (1984) are not supportive, probably because their nesting success studies were largely conducted on very good habitat for the length of their study.

The consequences of a rise in the proportion of late-hatched juveniles are several. Once a population is reliant on subsequent nesting attempts to offset adult mortality, there is little chance for the population to maintain itself. This is because the annual breeding pulse does not benefit from the increased clutch sizes of early nests and late-hatched individuals potentially enter winter with a reduced body mass and thus a reduced chance of survival.

Usable Space

There are 2 competing hypotheses in bobwhite management. The traditional approach has been to manage bobwhite on the basis of bobwhite density as a function of habitat quality, where quality exists in a continuum from poor to good. Conversely, Guthery (1997) offered the alternative hypothesis whereby mean bobwhite density increases as usability of space within a defined area increases.

If the use of habitat by bobwhite is a dichotomous response, with bobwhite entirely absent or present only at some density randomly fluctuating around a long-term mean, as Guthery (1997:294, 301) has suggested, declining regional abundance of bobwhite must be due to absolute loss rather than degradation of bobwhite habitat. Our analyses suggest an alternative possibility, largely because there is no reason to believe absolute loss of habitat should lead to any long-term changes in mean JPA. If bobwhite only occur in habitat attaining some threshold of suitability, as the hypothesis by Guthery et al. (2002) suggests, JPA should vary randomly around some non-varying mean. We however, observed long-term trends in this mean JPA. The gradual change in JPA that we observed suggests bobwhite abundance may begin to decline within continuously degraded habitat prior to their patch-level extirpation. To assess this observation more closely, we examined trends in mean abundance at occupied sites. After the effect of serial correlation was removed, NABBS counts at occupied survey sites demonstrated a within-site decline of $-1.48\%\cdot\text{yr}^{-1}$ (SE = 0.47%) (W. Thogmartin, *unpublished data*). A

significant portion of the serial correlation within the time series was due to annual abundance prior to 1971, but even after censoring these data the decline was a nontrivial -1.71%·yr^{-1} (SE = 0.33%). These declines are coincident with declining quality of habitat (Roseberry and Klimstra 1984, Brennan 1991, Warner 1994).

There is room, however, for accommodation of both the idea of habitat loss by Guthery et al. (2002) and our idea of habitat degradation as contributing to declining bobwhite populations. For instance, resumption of hatch proportion by the late 1990s to levels last seen in the 1960s may be due to hunters only hunting bobwhite in largely suitable, non-degraded habitat, the only huntable habitat remaining in Illinois. Roseberry and Sudkamp (1998) and Thogmartin (2002) reported significant associations of bobwhite presence and abundance to landscape scales. Thogmartin (2002:175) further theorized only 1/3 of suitable landscapes need be occupied to yield hypothesized state-wide population sizes. If habitat loss is a dynamic process within suitable landscapes, as it should be in a natural situation with land cover occurring in various successional states, then bobwhite may occur within landscapes as a metapopulation, moving from one patch to another as patches become available and then subsequently lost due to succession. However, in Illinois, a state with >80% of its land used for agricultural purposes, the natural situation hardly occurs. Rather, land is held at specific successional states, and thus gradual loss of habitat to succession does not occur over large scales. When habitat is lost, it is irrevocably lost. Prior to this loss, however, has been a degradation of agricultural habitat for bobwhite in the Midwest (Roseberry and Klimstra 1984, Warner 1994). Suitability of agricultural habitat for bobwhite has declined tremendously over the last several decades as agricultural practices have become increasingly efficient and fully implemented. Resumption of JPA to former levels may be an artifact of bobwhite only occurring in very restricted portions of their former range, in habitats having undergone less modification than the general agricultural landscape.

There were no obvious, long-term trends in sex ratios among juveniles or adults. Additionally, annual fluctuations were minor and seemingly unrelated to climatological or habitat conditions, and may therefore have simply reflected random variation. Furthermore, sex ratios seemed unrelated to other population parameters except for a weak tendency for declining populations to contain slightly more males among juveniles.

Hatching chronology, as indexed by the relative proportion of late-hatched juveniles in the fall population, increased from 1950 through the 1970's then stabilized. This shift toward later hatching dates appeared to coincide with a reduction in agricultural grasslands, especially hay. Because late clutches are generally smaller, reliance on renesting to compensate for failure of initial attempts could theoretically reduce productivity. Indeed, late hatches were often associated with annual population declines, and vice versa.

The ratio of juveniles per adult in fall populations declined from 1950 to about 1970, then stabilized over the remainder of the study. This trend was statistically associated with changes in gross amounts of agricultural grasslands (i.e., nesting cover) throughout the State and thus was apparently habitat related. The fact that populations declined over the last 30 years of study whereas JPA was relatively stable suggests habitat loss rather than deterioration. In contrast, declining JPA during the first 20 years of study may have reflected habitat deterioration prior to complete elimination. Short-term (annual) variation in this parameter was weather related with above-average summer precipitation and harsh winters leading to higher ratios. The latter relationship, which initially seems illogical, probably reflects the density-dependent nature of JPA and the fact that severe winters often were followed by very low breeding densities. Because JPA was strongly density-dependent, and integrated a variety of biological variables, the parameter was not a particularly good indicator of relative or absolute productivity or subsequent population size.

Table 10. Seasonal climate periods evaluated in multivariate regressions of demographic, harvest, and environmental parameters.

Period	Description
1 December-28 February	Winter
1 December-21 March	Winter
1 January-28 February	Late-winter
1 January-30 April	Winter-spring
22 March-20 April	Prenesting
1 May-19 July	Peak egg laying
21 April-18 August	Egg laying
20 June-18 August	Peak hatching
10 June-28 August	Hatching
30 June-28 August	Summer
1 June-28 August	Summer

Table 11. Summary statistics for northern bobwhite population data derived from wings collected from southern Illinois hunters, 1950-2001.

	JPA[1]	MA[2]	MJ[3]	KILL[4]	CKILL[5]	PREFAD[6]	H29[7]	H12[8]
Years	51	50	50	41	40	49	48	48
Mean	4.93	59.74	50.33	3.57	0.77	14.53	27.65	18.31
Median	4.77	59.61	50.47	3.62	-0.77	14.47	27.57	18.74
Minimum	2.82	45.98	46.01	2.33	-32.94	8.56	13.14	3.77
Maximum	7.95	67.76	53.47	4.94	49.93	22.39	40.58	28.74
SD	1.13	3.83	1.71	0.65	17.56	3.08	6.22	5.60

[1] Juveniles·adult^{-1}
[2] Percentage of males in the adult population
[3] Percentage of males in the juvenile population
[4] Number of bobwhite harvested·hunter trip^{-1}
[5] Percent change in KILL from the previous year
[6] Percentage of females that were adults in the previous year
[7] Percentage of hatch occurring after 29 July
[8] Percentage of hatch occurring after 12 August

Table 12. Spearman rank correlations between 4 indices of northern bobwhite abundance and 11 demographic parameters derived from harvested wings in Illinois (PREMA and PREMJ not shown). See Table 11 for definitions of response variable acronyms.

Abundance (*n* years)	JPA	MA	MJ	INDEX	KILL	CKILL	PRE JPA	PRE FAD	H29	H12	PRE KILL
NABBS (32)	-0.431*	-0.125	0.363*	-0.070	0.547**	-0.184	-0.199	0.298	-0.215	-0.217	0.659***
IDNR Counts (24)	-0.699***	-0.270	0.234	0.054	0.506*	-0.178	-0.330	0.287	-0.509*	-0.477*	0.557**
IDNR Harvest (24)	-0.431*	-0.110	0.226	0.290	0.737***	0.114	-0.147	0.124	-0.503*	-0.428*	0.400
CBC (32)	-0.317	0.185	0.445*	-0.198	0.295	-0.258	-0.039	0.037	0.034	-0.001	0.469**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 13. Environmental correlates to long-term trends in biological response parameters derived for northern bobwhite in Illinois, 1950-2001. JPA is the number of juveniles per adult, H29 is the proportion of juveniles hatched after 29 July, and KILL is number of birds killed per hunter trip, as derived from interviews and hunter-contributed northern bobwhite wings.

Response	Parameter	Estimate	Standard Error	t	P
JPA	Intercept	3.91	0.05	71.28	<0.0001
	Agricultural Grassland (ha) × 1000	0.0002	0.0000	20.15	<0.0001
H29: Model 1	Intercept	36.57	1.50	24.30	<0.0001
	Hay (ha) × 1000	-0.04	<0.01	-7.64	<0.0001
	Hay (ha)^2 × 1000	<0.01	<0.01	13.38	<0.0001
H29: Model 2	Intercept	50.24	3.32	15.13	<0.0001
	Agricultural Grassland (ha) × 1000	-0.01	<0.01	-7.90	<0.0001
	Agricultural Grassland (ha)^2 × 1000	<0.01	<0.01	10.35	<0.0001
KILL	Intercept	9.80	0.92	10.62	<0.0001
	Agricultural Grassland (ha) × 1000	<-0.01	<0.01	-9.02	<0.0001

Table 13. Continued.

Response	Parameter	Estimate	Standard Error	t	P
	Agricultural Grassland $(ha)^2 \times 1000$	<0.01	<0.01	11.89	<0.0001
	Precipitation (cm) During Hatch	-0.05	0.03	-1.80	0.0783

Table 14. Environmental correlates to annual variation in biological response parameters derived for northern bobwhite in Illinois, 1950-2001.

Response	Parameter	Estimate	Standard Error	t	P
JPA	Intercept	5.91	1.41	4.20	0.0002
	Precipitation During Peak Hatch	0.11	0.06	2.03	0.0496
	Mean Winter Temperature	-0.13	0.03	-3.99	0.0003
	Kill Per Trip in Year(t-1)	-0.74	0.20	-3.68	0.0007
H29	Intercept	-12.61	9.03	-1.40	0.1694
	Potential Evapotranspiration in January	-23.04	11.07	-2.08	0.0429
	Potential Evapotranspiration in August	4.57	2.31	1.98	0.0539

Table 14. Continued.

Response	Parameter	Estimate	Standard Error	t	P
KILL	Intercept	-14.1665	4.5448	-3.1171	0.0038
	Kill Per Trip in Year(t-1)	0.3869	0.1404	2.7544	0.0095
	Number of days of snow > 2.5 cm	-0.0113	0.0050	-2.2781	0.0293
	Minimum Temperature in June (°C)	0.0652	0.0346	1.8837	0.0684
	Mean Temperature in July (°C)	0.0967	0.0414	2.3324	0.0259
	Potential Evapotranspiration in August[@]	0.2291	0.1462	1.5667	0.1267
	Potential Evapotranspiration in November[#]	0.8089	0.3578	2.2606	0.0305

[#] Exclusion of this variable resulted in a model with an AICc 0.16 units from the full model.
[@] Exclusion of this variable and Evapotranspiration in November resulted in a model with an AICc 2.33 units from the full model.

Table 15. Ranking of informative models relating effects of climate on annual variation in the proportion of late-hatched northern bobwhite juveniles in Illinois, 1950-2001. Models were ranked by AIC_c and normalized AIC_c weights ($\hat{w}_i$).

Model Parameters	K[a]	AIC_c	ΔAIC_c	$\hat{w}_i$
August Evapotranspiration + January Evapotranspiration	2	227.42	0	0.518
January Evapotranspiration	1	229.25	1.83	0.207
August Evapotranspiration	1	229.67	2.25	0.168
August Mean Temperature	1	231.47	4.05	0.068
Null	0	232.63	5.21	0.038

[a] Number of estimable parameters.
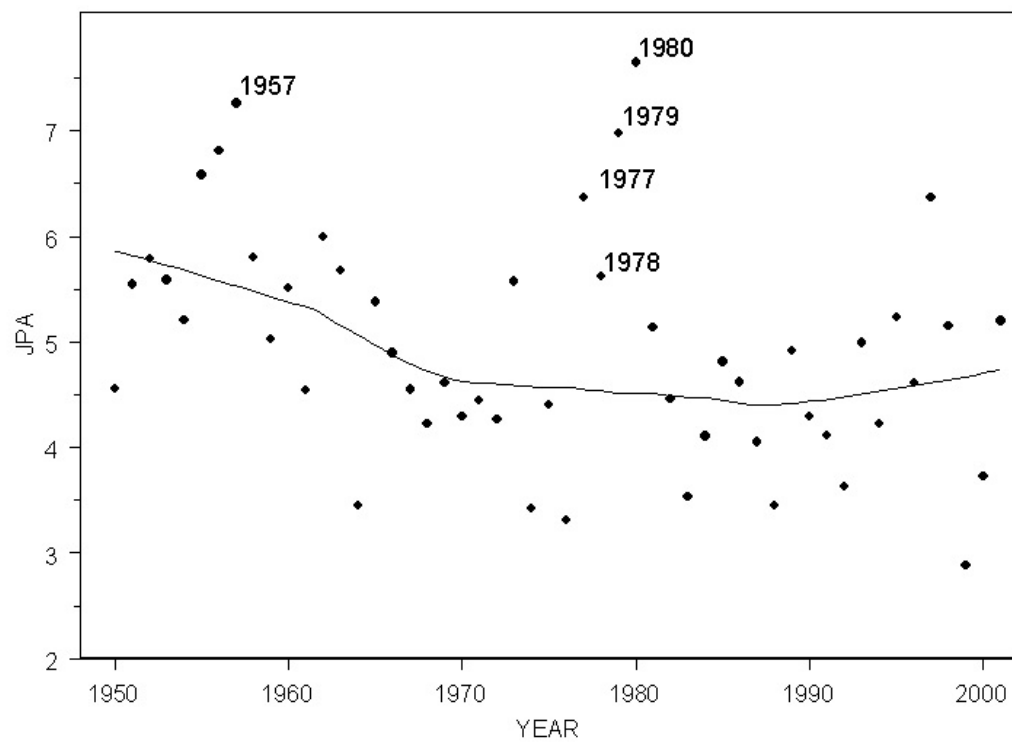
Figure 13. Temporal trend in juveniles·adult^{-1} between 1950 and 2002. Line is a locally-weighted regression fitted to the trend.
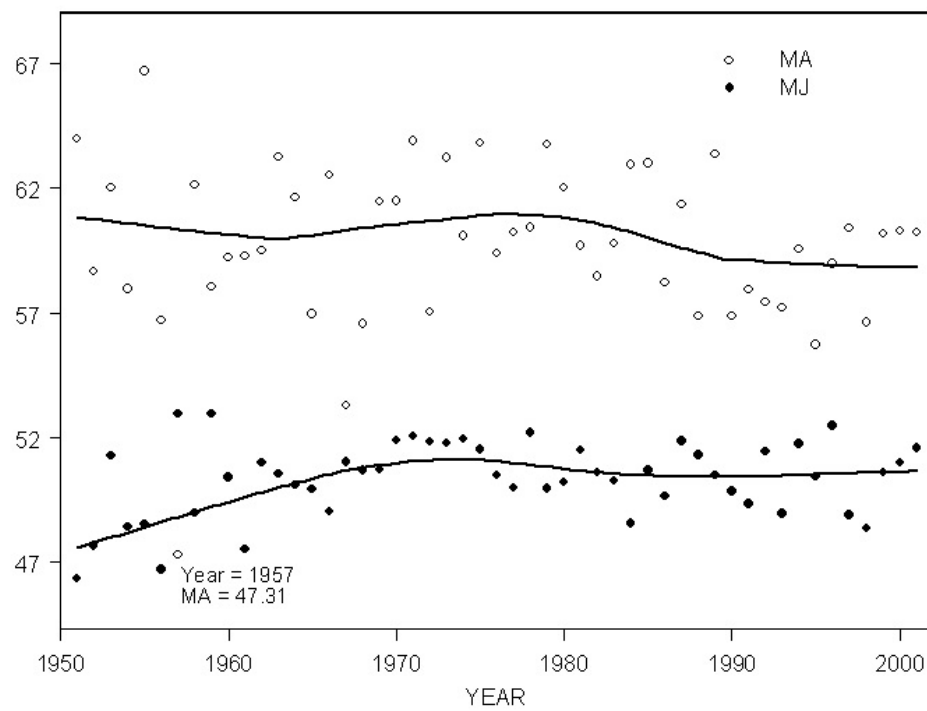
Figure 14. Temporal trends in within age-group sex ratio between 1950 and 2002. Line is a locally-weighted regression fitted to the trend.
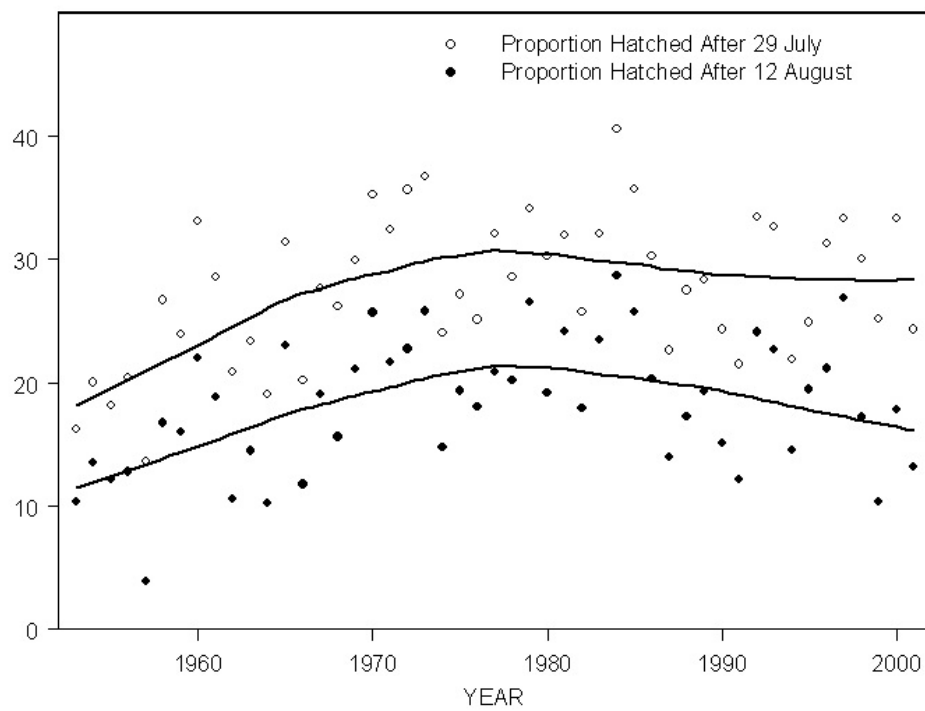
Figure 15. Proportion of juveniles hatched late in the nesting season between 1952 and 2001. Line is a locally-weighted regression fitted to the trend in each time series.
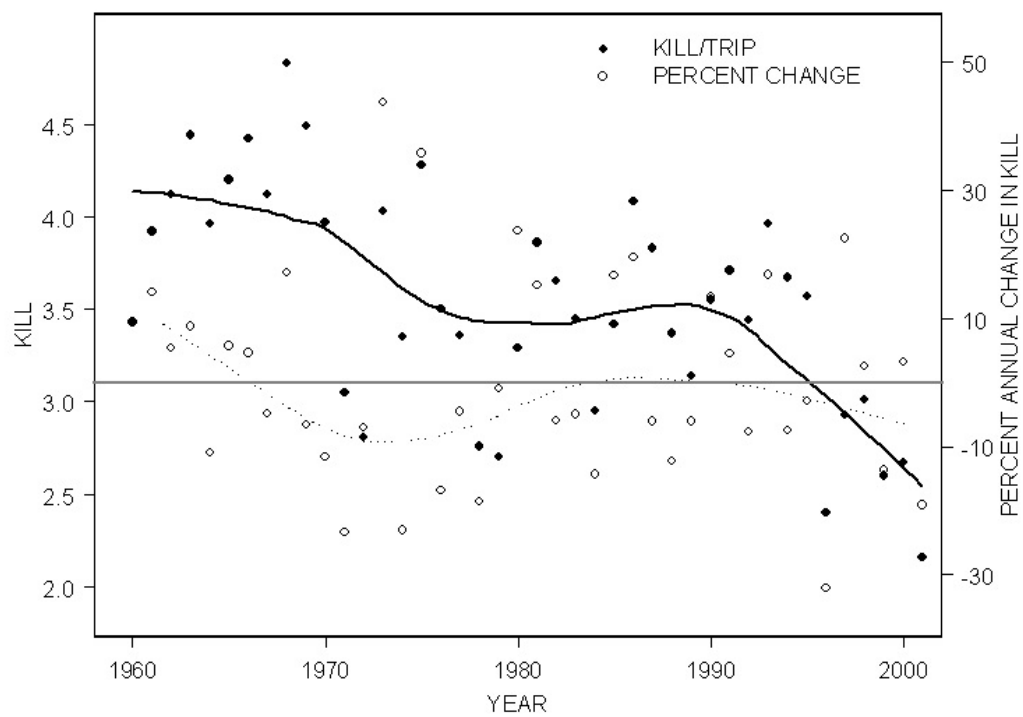
Figure 16. Temporal patterns in kill per trip and percent annual change in kill per trip between 1960 and 2002. Curves are locally-weighted regressions fitted to the trends; horizontal straight line denotes 0% change in annual kill.

90
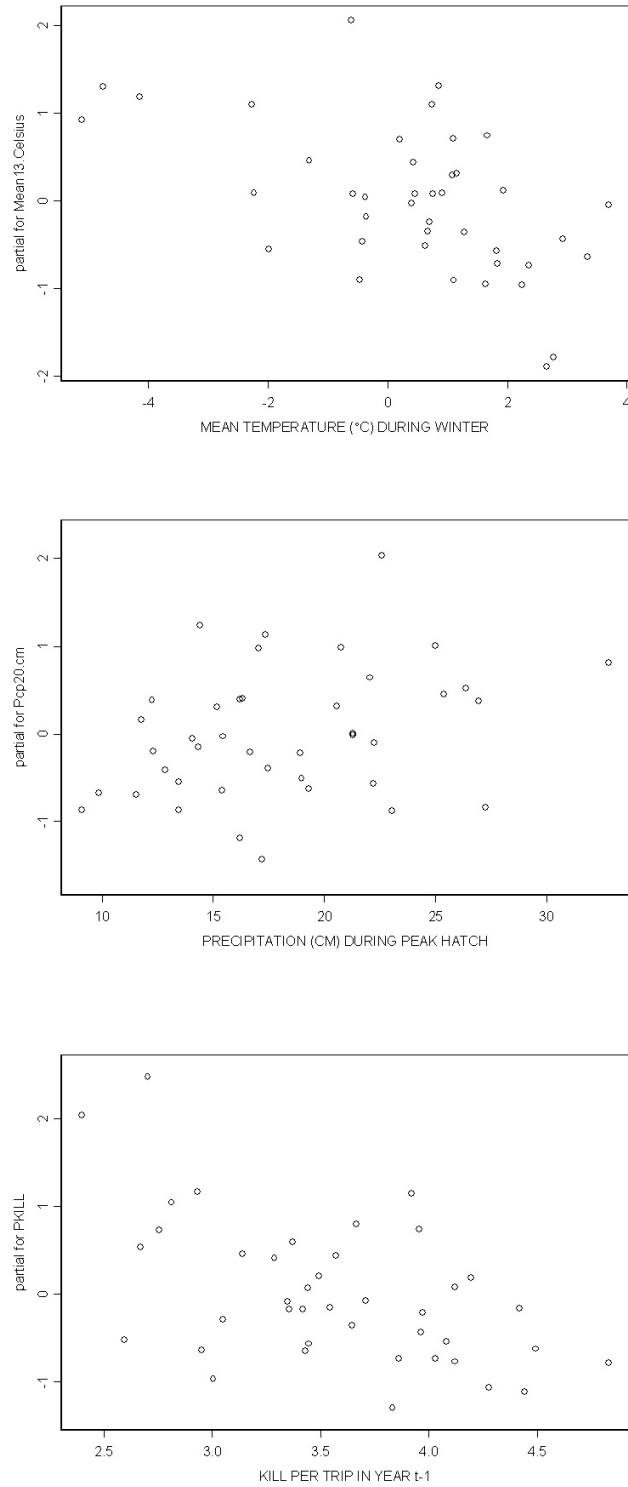
Figure 17. Partial regression plots for relationship between environmental correlates and number of northern bobwhite juveniles per adult in Illinois between 1950 and 2001.

JOB R-1.3: ANALYZE AND REPORT

Objectives: (1) To analyze results and prepare reports for Jobs 1.1 and 1.2 and report; and (2) to report and discuss findings in a timely manner.

Requirements for this job have been met with findings and recommendations in Annual Performance Reports and the Final Project Report for Job R-1.2. In addition, Illinois Department of Natural Resources, Division of Wildlife Resources program staff have been advised of interim findings in a timely manner by means of both formal meetings and informal discussions. The following list identifies theses, manuscripts, and professional papers presented on research conducted under the auspices of this Federal Aid project:

Roseberry, J. L., and W. L. Weber. 2000. The Conservation Reserve Program and northern bobwhites in Illinois. Farm Bill Briefing Session, North American Wildlife and Natural Resources Conference, Chicago, Illinois, USA.

Thogmartin, W. E. 2002. Spatio-temporal dynamics of northern bobwhite (*Colinus virginianus*) in Illinois. Dissertation, Southern Illinois University, Carbondale, Illinois, USA.

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Weber, W. L. 2000. Contribution of the Conservation Reserve Program to upland wildlife habitat and general landscape structure in Illinois. Thesis, Southern Illinois University, Carbondale, Illinois, USA.

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Appendix 1. 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 1. 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	8	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
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

Appendix 1. Continued.

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
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
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

Appendix 1. Continued.

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
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
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

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
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
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

Appendix 1. Continued.

Rank	Easting	Northing	Network ID	No. of Neighbors	Proportion Unoccupied	Patch Size (ha)	HSI
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

ATTACHMENT

WEBER 2002