LAND COVER AND BOBWHITE ABUNDANCE ON OKLAHOMA FARMS AND RANCHES

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Abstract: To test prevailing paradigms of habitat management for northern bobwhites (*Colinus virginianus*), we analyzed relations between the abundance of these birds, land-cover classes, and landscape metrics on Oklahoma farms and ranches (200-ha areas; $n = 78$) during 1998–1999. Based on replicated call-count indices, bobwhites declined (–0.03 to –0.07 males/ha; 95% confidence level here and below) with the quantity of an area in mature woodland, and increased (0.02 to 0.05 males/ha) with the quantity of brushy prairie or early successional woodland. We observed highest populations in the absence of cropland agriculture. Bobwhites declined as Shannon diversity of cover types (–6.0 to –0.01 males/Shannon unit), patch richness (–0.08 to –0.02 males/patch), and the density of woody edge (–0.027 to –0.003 males/m/ha) increased. Bobwhites responded more strongly to the composition of land-cover classes on areas than to the configuration of these classes in areas. Our results did not support the patchwork agriculture model of bobwhite abundance or the principle of edge. Results were consistent with a hypothesis that predicts bobwhite abundance is a nondecreasing function of usable space in time.

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The general relations between land-use practices and northern bobwhite populations were first reported in the 1930s (Stoddard 1931, Leopold 1933, Errington and Hamerstrom 1936, Lehmann 1937). The work of these pioneers subsequently was followed by numerous studies that have expanded management knowledge. At this time, a great deal is known about the management of habitat for bobwhite populations.

What remains to be learned has less to do with the cause-effect habitat processes governing bobwhite populations and more to do with the nature and strength of relationships between habitat features and bobwhite population abundance. Moreover, some management hypotheses put forth by the pioneers have not been adequately tested through critical experimentation.

As examples, Leopold's patchwork agriculture model of bobwhite abundance (1933:307) and law of dispersion (principle of edge; 1933:132) have been taken as standards in the management of bobwhite habitat. However, research through the years has questioned these management hypotheses. The patchwork agriculture model did not hold for bobwhites in Wisconsin in the 1840s–1850s (Schorger 1946). Bobwhites reached exceptional densities before patchwork agriculture had any appreciable effect on Wisconsin landscapes. Currently, some of the strongest bobwhite populations in the continental United States (north Texas, south Texas, western Oklahoma) occur on rangeland where cropland agriculture is rare or absent.

The principle of edge, elevated to a theorem by usage rather than by experimentation (Giles 1978:13), is a special circumstance within a more general outlook on bobwhite abundance, namely the quantity of usable space in time (Guthery 1997). Theoretical reasoning suggests that an infinite variety of patch (woody cover, herbaceous cover) configurations may be optimal for bobwhites (Guthery 1999). It follows that within these configurations, no relation exists between the abundance of bobwhites and edge that is meaningful to this species; i.e., expected abundance would remain constant as the quantity of edge varies. Guthery and Bingham (1992) recognized that no relation may exist between the abundance of edge-obligate animals and the quantity of edge within a certain range (domain) for quantity of edge. They pointed out, more-

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over, that it is possible for edge-obligate animals to decline as the quantity of edge increases.

We studied the relation between bobwhite abundance, land cover, and landscape metrics on Oklahoma farms and ranches. Because we used multiple observers to conduct call-counts, we assessed the comparability of counts made by different observers. We then related bobwhite abundance to the composition and structure of land cover on 200-ha areas to quantify situations that enhanced and inhibited bobwhite populations. Our data permitted us to test Leopold's (1933) patchwork agriculture model of bobwhite abundance and law of dispersion and Guthery's (1997, 1999) space–time hypothesis of bobwhite abundance. Briefly, the latter hypothesis states that bobwhite abundance on an area is a simple, nondecreasing function of the amount of permanent, suitable cover for bobwhites on the area. Habitat quality—as gauged by interspersion, diversity, edge density, and food supplies—plays a secondary role to habitat quantity in governing bobwhite abundance under the space–time hypothesis.

STUDY AREAS AND METHODS

We obtained data from 78 sites in central and western Oklahoma during 1998 and 1999. The study area included a rectangle bounded by latitudes 36°16′33″N and 34°10′27″N and by longitudes 99°52′51″W and 97°08′36″W. Sites in central Oklahoma (n = 68) were in the Cross Timbers Forest Type and Tallgrass Prairie Type, whereas sites in western Oklahoma (n = 10) were in the Sandsage (*Artemisia filifolia*)–Grassland Type (Duck and Fletcher 1943). Cross Timbers vegetation is deciduous woodland consisting primarily of post (*Quercus stellata*) and blackjack oak (*Q. marilandica*) that develops closed canopies with age. Warm-season tallgrasses characterize openings in Cross Timbers forests. Eastern red cedar (*Juniperus virginiana*) has invaded openings in the Cross Timbers in recent years, resulting in further closure of the woody canopy. Duck and Fletcher (1943) provided information on climate, soils, and vegetation of these types.

We arbitrarily selected sites that gave a broad range in land cover characteristics (100% cropland–100% noncrop vegetation). We attempted to select sites equinumerously according to quintiles of cropland (0–20%, >20–40%, ...). We were less interested in whether certain variables, such as permanent cover, influenced the abundance of bobwhites because a large body of research results demonstrates such variables are influential (Guthery 1997). We were more interested in the validity of management paradigms and the strength and nature of the relationships (Edwards 1992:2) between bobwhite abundance and land cover and structure.

Call-counts

We conducted repeated call-counts (5–7 replications/site/year) during May–June 1998 and 1999 on each site. Counts took place from approximately sunrise to 1000 hr. This timing encompassed daily periods of peak calling activity based on concurrent research on the calling behavior of bobwhite males (Wilson 2000). We recorded the number of different males heard calling and the number of calls over a 6-min listening period. We conducted the first 3 min in a standard call-count manner (Elder 1956). At the end of the first 3 min, we broadcast an assembly call (Coody 1991) at 90 dB in the 4 cardinal directions, listened for 1.5 min, broadcast the assembly call again, and listened an additional 1.5 min. We calculated mean males/site for each year and used these 2 means to calculate a mean over the 2 years. This latter, 2-year mean of means was used as the dependent variable in simple linear regression analysis of relations between bobwhite abundance and land cover and structure. Use of the 2-year mean invoked normality by virtue of the central limit theorem (the distribution of means from any distribution tends to normality; Mendenhall et al. 1990:319).

Call-counts were conducted by 10 observers in 1998 and 8 observers in 1999. Therefore, we needed to determine whether counts among observers were comparable because if the counts were not comparable, variation could accrue from the observer, independent of variation accruing from the landscapes under study. We used 1 observer (control) in each year to conduct counts with other observers (test); the control observers differed between years. We then regressed the total number of males and total calls heard by the control observer (x) against these variables for the test observers (y) under a zero-intercept, linear model (the point $x = y = 0$ should exist; i.e., if an area has no quail, neither the control nor the test observer should hear any). A significant linear relationship with a slope not different from 1.0 indicated comparability among observers, whereas a positive slope different from 1.0 indicated a correlation among observers. We analyzed mean and maximum counts on sites between years to determine count repeatability and site consistency.

Site Analysis

We obtained recent aerial photographs (black and white, 1:7,920) of study sites from the U.S. Department of Agriculture, Farm Services Agency. The aerial photographs were used to develop overlays of land cover types on each site within radii of 400 m and 800 m from a listening post. Because land cover was similar for 400- and 800-m radii, and because bobwhite males may be heard up to about 800 m (Bennitt 1951), we report landscape results from the 800-m radius (200 ha). Each site was visited to verify land-cover classifications. These classifications included cereal crops; peanuts; cropland not in cereals or peanuts; pecan orchards; tame pastures (3 cover types) consisting of Bermudagrass (*Cynodon dactylon*), weeping lovegrass (*Eragrostis curvula*), or Old World bluestems (*Bothriochloa* spp.); Conservation Reserve Program (CRP) fields; mature Cross Timbers vegetation; brushy prairie (mixed brushland and prairie, including early-successional woodland); native prairie dominated by bluestems (*Andropogon gerardii* and *Schizachyrium scoparium*); riparian zones; marshes and wetlands; water; and human developments. Brushy prairie and early-successional woodland had, by ocular estimate, 10–25% canopy coverage of brush generally <2 m tall. Native prairie consisted primarily of warm-season tallgrasses with <5% brush coverage. These 15 land-cover classifications were used for analysis of landscape structure.

We collapsed the classifications to 7 categories for composition analysis: cereals; cropland other than cereals; tame pasture (Bermudagrass, lovegrass, Old World bluestems, and CRP fields); brushy prairie; native prairie; woodland (mature Cross Timbers, riparian zones, and pecan orchards); and other (marshes and wetlands, water, human developments). Conservation Reserve Program fields were included in tame pastures because these fields typically are planted to Old World bluestems or weeping lovegrass in central and western Oklahoma.

We placed clear mylar sheets over each aerial photograph, and traced land-cover polygons onto the overlays for scanning. We digitized completed overlays using a digital scanner and hand digitizing. We edited, rectified, and vectorized scanned images using Line Trace Plus version 2.2 (U.S. Department of Agriculture, Washington, D.C., USA) within a UNIX environment. We used Arc/INFO and PC ArcView (ESRI, Redlands, California, USA) to create land-cover maps. Supervised photo interpretation was used to label each land-cover type. We used FRAGSTATS (McGarigal and Marks 1994) to estimate landscape metrics for each study site. The 20 metrics were submitted to factor analysis (Afifi and Clark 1984) to identify groups of intercorrelated metrics to reduce dimensions of the data set. If several variables are correlated with each other, an analysis of any 1 of them provides information on all of the others; verbal and scientific parsimony is served, therefore, by reducing the dimensions of a data set. We arbitrarily used the metric with the highest absolute loading on a given factor for discussion of the effects of landscape structure on the call-count index. Note that variables with high loadings on 1 factor are not correlated with variables with high loadings on other factors.

Tests and Inference

Bobwhite abundance should be related positively and linearly to the density of woody edge (m/ha) if Leopold's (1933:132) law of dispersion holds. Therefore, to test this law, we classified brushy prairie, Cross Timbers, riparian zones, and pecan orchards as woody cover and estimated woody edge density (m/ha) for each site with PC ArcView. We then analyzed the relation between the mean call-count index and woody edge with linear regression.

We used a simple, artificial neural network model (Hagan et al. 1996) to examine the composite effects of land cover and structure. Neural modeling is analogous to multiple regression, but it is more powerful because it is insensitive to assumptions about normality (nonparametric) and multicollinearity; neural modeling deals equally well with linear and nonlinear relationships (Smith 1996). The independent variables were the combined hectarage of brushy and native prairie (permanent cover to which bobwhites are adapted) and the number of cover patches on a site (an indirect measure of interspersion and diversity). The backpropagation model consisted of 2 processing elements (hidden nodes). We randomly selected 80% of the data for developing the model and used the remaining 20% to test the model.

If the space–time hypothesis has merit, then bobwhite abundance should show a positive trend with the quantity of permanent cover to which they are adapted on study areas. This trend was tested for brushy prairie with linear regression and for permanent native cover with the neural model. Moreover, under the space–time hypothesis, habitat quality variables as measured

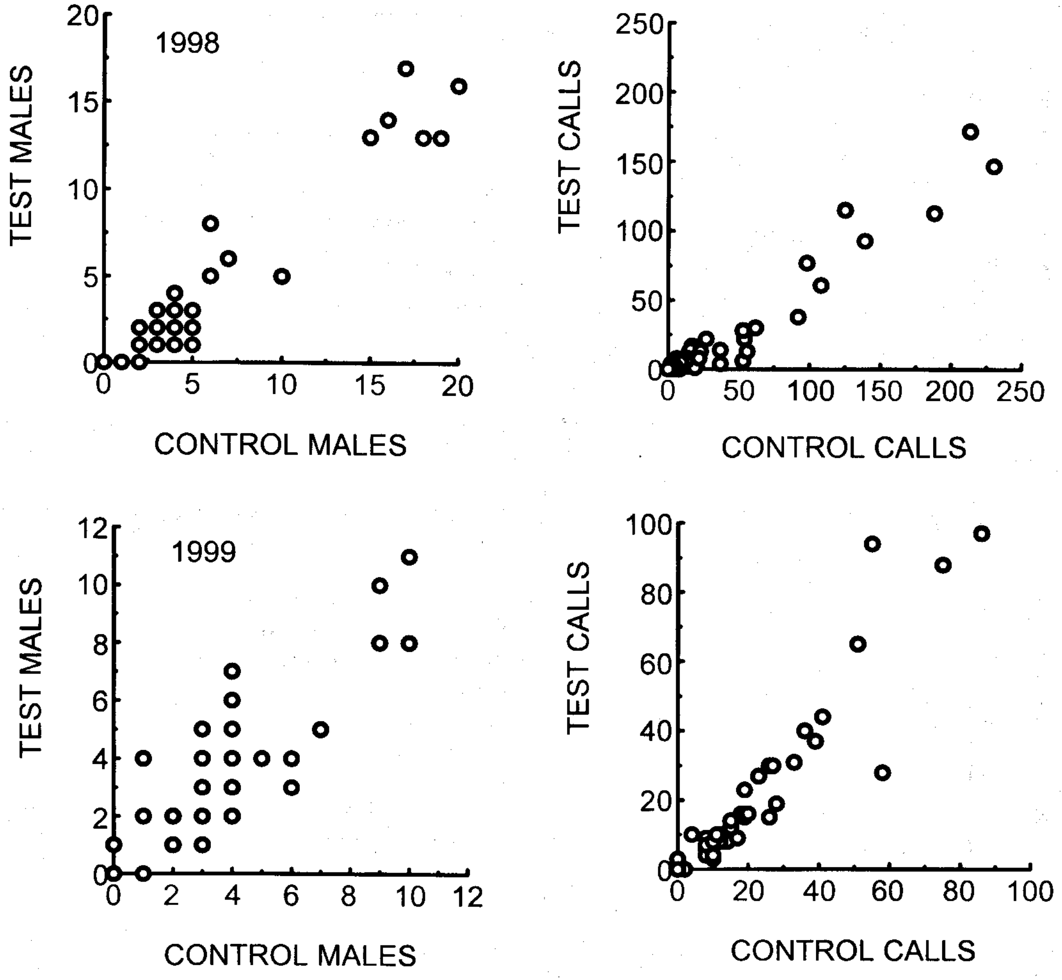

Fig. 1. Relation between the total number of northern bobwhite males and the total number of calls heard by control and test observers during 6-min periods at listening posts in central and western Oklahoma, USA, 1998 and 1999.

in our study (interspersion, diversity, patch richness) should be largely inconsequential in explaining abundance.

In keeping with recent recommendations to economize on significance testing and reporting (Cherry 1998, Johnson 1999), we approached inference from a 95% CL standpoint. Results for regression and correlation analyses were considered useful at $P < 0.05$.

RESULTS

Call-counts

The call-count index (males/site; 2-yr mean of means) was associated with considerable variation among sites ($\bar{x}$ = 4.2 ± 3.87 [SD], CV = 92.1%). The range in the index was 0.1–15.9 males/site. The grand mean retained approximately the same amount of variation as the year-specific means ($\bar{x}$ = 4.1 ± 3.10, CV = 75.6% in 1998; $\bar{x}$ = 4.3 ± 5.35, CV = 124.4% in 1999).

The linear, zero-intercept relations between the control and test observers for the number of males and number of calls heard at listening posts were strong ($r \geq 0.87$) for each year of study (Fig. 1). This outcome indicated comparability among observers, because a correlation between 1 observer and all others indicates mathematically a correlation between any 2 of the test observers.

However, the relations between the control and test observers were different in the 2 years. In 1998, total males ($y = 0.76x$) and total calls ($y =$

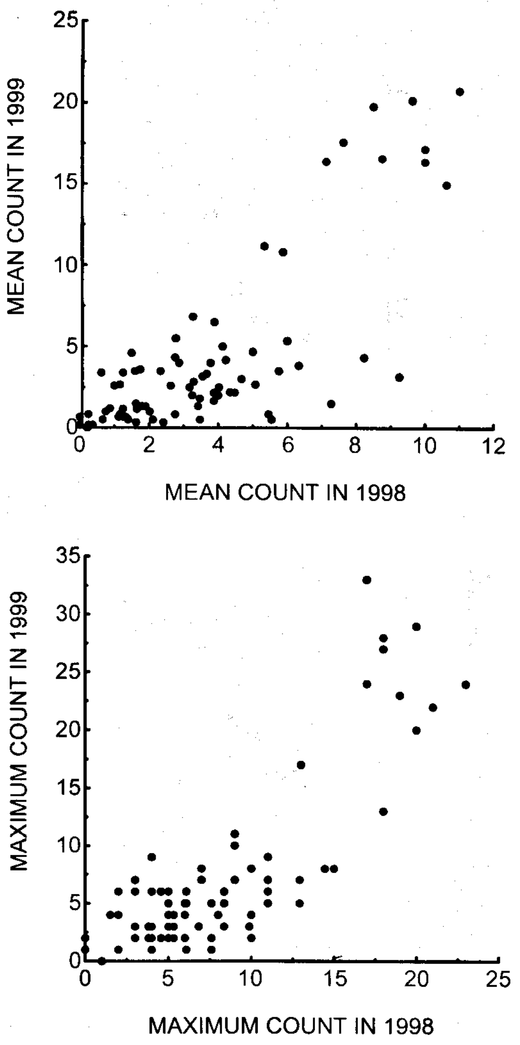

Fig. 2. Relation between the mean number of bobwhite males heard calling during 6-min periods at 78 sites in central and western Oklahoma, USA, during 1998–1999 (5–7 counts/site/year).

0.66x) indicated the control observer (x) heard more males and calls than the test observers (y). The 95% CL for these slopes were 0.71–0.82 and 0.61–0.70. For example, the average difference in males heard (control observer – test observer) was 1.38 ± 0.21 (SE, $n = 54$) in 1998. In 1999, the total males relation was $y = 0.94x$ (95% CL = 0.85–1.04), and the total calls relation was $y = 1.07x$ (95% CL = 0.97–1.17, $n = 40$). The average difference in total males was 0.05 ± 0.21 in 1999. We corrected counts ($n = 22$) by the control observer in 1998 for the analyses that follow; these corrections standardized counts among observers for 1998. There was no need to standardize counts with the 1999 data.

Comparison of corrected counts between years indicated that the call-count index provided repeatable information on the abundance of calling males at sites (Fig. 2). The linear correlation ($n = 78$) between means was 0.78, and the correlation between maximums was 0.83.

Site Analysis

Composition.—We found no relation between the call-count index and the quantity (ha) of cereals, other crops, tame pasture, or native prairie (Figs. 3A–3D). The call-count index increased with the area of brushy prairie at a rate of 0.04 males/ha (95% CL = 0.02–0.05 male/ha, $r = 0.52$; Fig. 3E). Each additional hectare of mature woodland subtracted 0.05 males from the call index (95% CL = –0.07 to –0.03 males/ha, $r = -0.52$; Fig. 3F).

We did not analyze the influence of other habitat types (marshes and wetlands, water, human developments) on the call index. This land-cover classification (other) represented low percentages (<5%) of all study sites, and therefore would not be expected to explain variation in the call index.

Structure.—Factor analysis revealed 4 factors that explained 82% of the total variation in the landscape metrics (Table 1). We interpreted the factors as diversity (38.8% of variation), patch-size variability (25.4%), patch richness (10.8%), and patch shape (7.0%). Variables with the highest absolute loadings on the 4 factors were the Shannon diversity index, coefficient of variation on patch size, patch richness (number of different patches on a site), and mean shape index (Table 1).

No relation existed between the call-count index and the coefficient of variation in patch size or the mean shape index (Figs. 4B,D) for study sites. The regression coefficient indicated a decline of 3 males for each unit increase in Shannon diversity ($r = -0.22$, 95% CL = –6.0 to –0.01 males/Shannon unit; Fig. 4A). Likewise, the index declined at –0.05 males/patch ($r = -0.33$, 95% CL = –0.08 to –0.02; Fig. 4C). Finally, the call-count index declined at a rate of 0.02 males/m/ha (95% CL) as the density of woody edge increased ($r = -0.28$, 95% CL = –0.027 to –0.003; Fig. 5).

Composite Effects.—The correlation between the observed call-count indices and those predicted by the neural model was $r = 0.57$ for the training data set ($n = 62$ randomly selected observations).

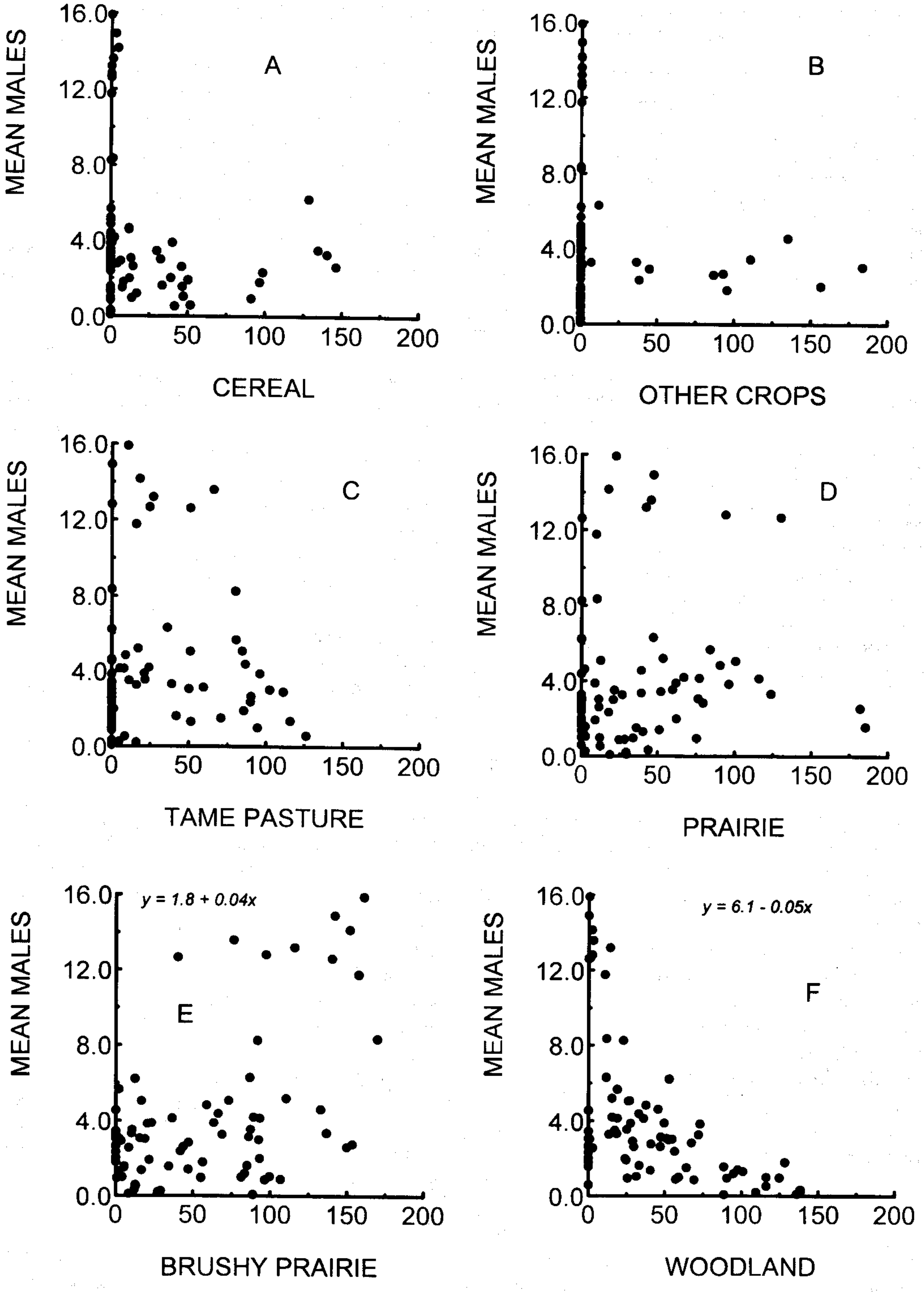

Fig. 3. Relation between the mean number of bobwhite males heard calling during 6-min periods and land cover variables (ha) within an 800-m radius of the listening post at 78 sites in central and western Oklahoma, USA, 1998 and 1999. A regression equation is given for significant ($P < 0.05$) relationships.

Table 1. Factor loadings for landscape metrics derived from 78 200-ha areas in central and western Oklahoma, USA, 1998–1999.

Metric	Factor I	Factor II	Factor III	Factor IV
Number of patches	0.46	–0.78	–0.19	0.03
Largest patch index	–0.48	–0.28	0.44	0.42
Patch density (no./100 ha)	0.46	–0.78	–0.19	0.02
Mean patch size (ha)	–0.67	0.62	0.10	0.10
Mean shape index	–0.31	–0.10	0.15	–0.79
Area-weighted mean shape index	0.19	–0.83	0.07	0.07
Double log fractal dimension	0.26	–0.39	0.02	0.41
Mean patch fractal dimension	0.16	–0.80	–0.40	–0.40
Area-weighted mean patch fractal dimension	0.44	–0.81	–0.01	–0.07
Patch size standard deviation	–0.75	0.27	0.31	0.30
Patch size coefficient of variation	0.03	–0.86	0.18	0.34
Patch richness	0.67	0.09	0.72	–0.06
Patch richness density (no./100 ha)	0.67	0.09	0.72	–0.06
Relative patch richness (%)	0.67	0.09	0.72	–0.06
Shannon diversity	0.93	0.28	0.13	0.02
Simpson diversity	0.92	0.32	–0.08	0.06
Modified Simpson diversity	0.92	0.32	–0.06	0.06
Shannon evenness	0.85	0.35	–0.26	0.07
Simpson evenness	0.88	0.34	–0.23	0.09
Modified Simpson evenness	0.82	0.35	–0.34	0.10

The model also performed acceptably ($r = 0.58$) on 16 random observations reserved for testing it.

The neural model indicated that, holding the number of habitat patches constant at any value, the call-count index increased curvilinearly with the quantity of permanent cover (Fig. 6). Conversely, the model predicted a declining call-count index for any level of permanent cover as the number of patches increased. The effect of permanent cover was stronger than the effect of number of patches because there was a larger range of predictions along the permanent cover axis than along the number-of-patches axis. The predicted call-count index maximized at maximal amounts of permanent cover and minimal numbers of patches.

DISCUSSION

Call-counts

Our analysis, like those of previous workers who used call-counts of bobwhite abundance (Church et al. 1993, Roseberry and David 1994, Brady et al. 1998), was based on the assumption that call-counts are a valid index of population abundance. This assumption could fail because of variability among observers, variability in the calling behavior of males, and site effects that influence the propagation of sound.

Variability among observers in the number of males heard at listening points may arise from ≥2 sources. During 1998, a large but undetermined portion of the variability could be attributed to the control observer; additional variability undoubtedly arose from subjective identification of individual males (given the same calling background, counts of observers may differ because of differences in interpretation of the number of males calling). During 1999, most variability in males heard by observers seemed to arise from identification of individual bobwhites because there was essentially a 1:1 relation between total males and total calls between control and test observers and because the average difference in total males was essentially zero. In other words, subjective interpretation of the number of calling males was the only explanation for variation between the control and test observers in 1999. Otherwise, we observed strong correlations between observers in the estimated number of males and total calls heard (Fig. 1) and the call-count index was repeatable among sites between years (Fig. 2).

We used the substantial body of information on bobwhite–habitat relations collected during the last 70+ years (reviewed in Guthery 1997) to select sites expected to contain bobwhite populations ranging from low to high. The call-count results were consistent with these expectations; i.e., higher populations of calling males were associated with higher quantities of suitable cover (Figs. 3E, 6).

So we have no reason to suspect that our index was an invalid metric for the population of calling males, the dependent variable in our modeling exercises. However, we would expect more nebulosity to accrue in using the calling-male index to predict fall population abundance. Norton et al. (1961), in an evaluation of data collected by Bennitt (1951), Reeves (1954), and Rosene (1957), argued that call-counts were a poor predictor of the autumn population, due in large part to variation in production among years. Conversely, Ellis et al. (1972) and Snyder (1984) considered the call index reliable for bobwhites, Gallizioli (1965) for Gambel's quail (*Callipepla gambelii*), and Brown et al. (1978) for scaled quail (*C. squamata*). Thus, whereas strength of the relation between the call-count index and

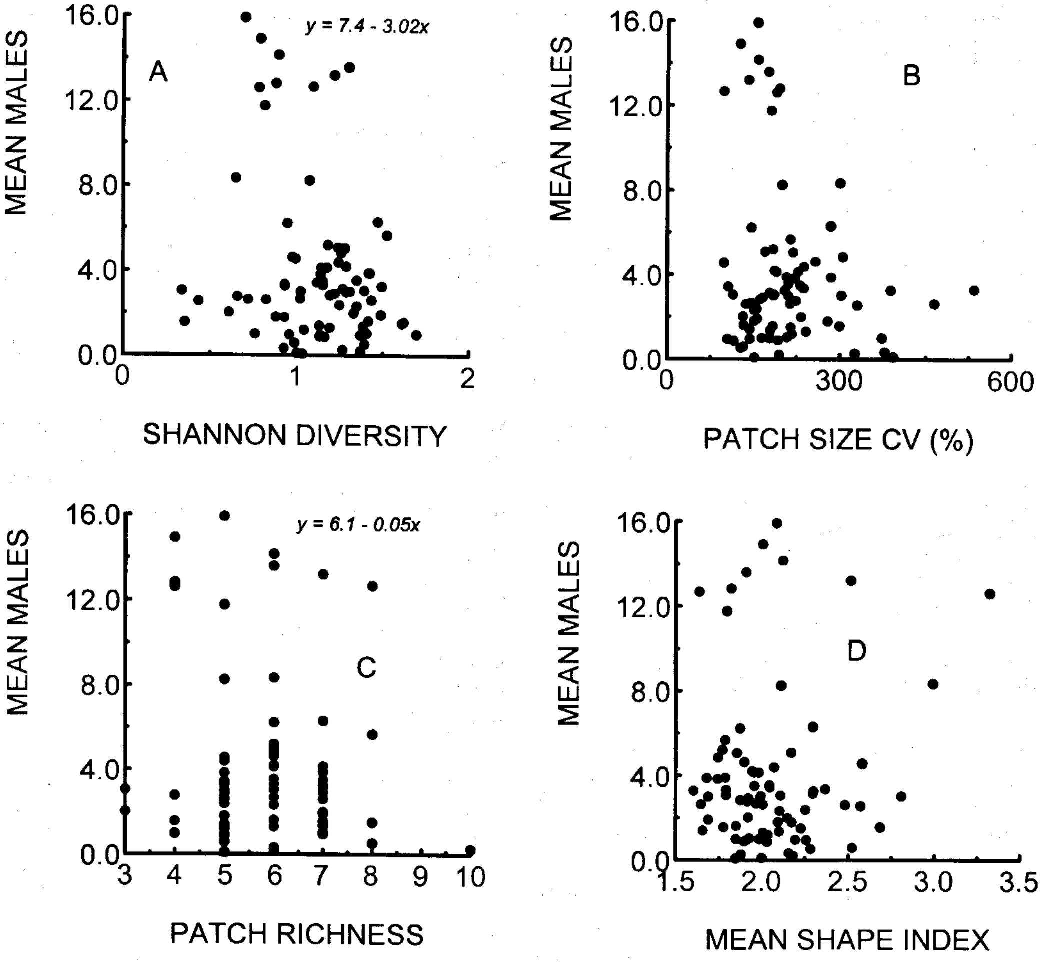

Fig. 4. Relation between the mean number of bobwhite males heard calling during 6-min periods and selected landscape metrics within an 800-m radius of the listening post at 78 sites in central and western Oklahoma, USA, 1998 and 1999. A regression equation is given for significant ($P < 0.05$) relationships.

autumn abundance is variable, existence of the relation does not seem to be in question.

A final source of variation in the call-count index was variability in factors that affect the propagation of sound waves and therefore the area over which calling males may be heard. Laws of physics dictate that air temperature, humidity, wind speed, and vegetation influence the propagation of sound waves (Wiley and Richards 1982) and the human-perceived calling activity of bobwhite males (Wilson 2000). Given a constant number of calling males, variation in these factors among sites could influence the number of males heard on sites. We attempted to reduce these effects with replicate sampling at sites and use of call playbacks (Coody 1991). However, the possibility remains that the radius of audibility was lower in areas with higher percentages of woodland vegetation because of sound-absorption effects. This could have induced bias in our assessment of the effects of woodland on bobwhite abundance.

Landscape Analysis

Competing Hypotheses.—Our study sites were widely separated geographically. Sites with higher call-count indices largely were limited to western portions of Oklahoma. Thus, geographical differences associated with weather patterns or geologic substrates could have influenced our findings. We note, however, that certain sites in north–central and south–central Oklahoma had

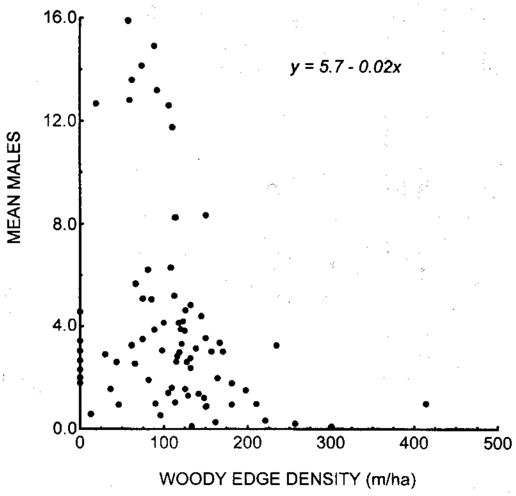

Fig. 5. Relation between the mean number of bobwhite males heard calling during 6-min periods and the density of woody edge at 78 sites in central and western Oklahoma, USA, 1998 and 1999.

high mean call-indices in ≥1 year of study. These sites had landscapes consistent with those in western Oklahoma (brushy prairie and native prairie with small amounts of tame pasture, cropland, and woodland). Thus, we obtained evidence of landscape composition effects that were independent of geographic location.

Variability in predator populations, including human predators, possibly contributed to the variation in call-indices among sites. Sites with lower bobwhite populations had higher values for Shannon diversity (Fig. 4A), patch richness (Fig. 4C), woody edge (Fig. 5), and number of patches (Fig. 6). These conditions (high edge density) could foster nest depredation (Hartley and Hunter 1998, Brand and George 2000) and reduce bobwhite abundance.

Sites in western Oklahoma, which attained the highest mean call-indices, were open to public hunting and 6 sites in south–central Oklahoma that had high call-indices in 1998 were operated under lease hunting. Thus, we had evidence that relatively intense hunting pressure was compatible with strong bobwhite populations, as gauged by summer call-counts.

Comparison with Other Studies.—Previous work on the relation between landscape composition and structure includes Brady et al. (1993, 1998) and Roseberry and Sudkamp (1998). Our results were not directly comparable to the results of these studies in some cases. For example, our study sites were devoid of row crops, such as sorghum, soybeans, and corn, which were present in the studies cited. Our findings were consistent in that bobwhites exhibited a positive response to rangeland (Brady et al. 1998). Likewise, the scatter plots of a bobwhite abundance index versus grassland of Roseberry and Sudkamp (1998; Figs. 1, 2) were similar to our scatter plots for tame pasture and prairie (Figs. 3C,D). Contrary to Brady et al. (1993, 1998), we found wheat (cereal crops) and woodland to be negatively associated with bobwhite populations. Roseberry and Sudkamp (1998) found landscape contagion, which was virtually a linearly scaled version of Shannon evenness in their data, to be diagnostic of bobwhite abundance. We observed an effect of Shannon diversity in our study (Fig. 6), which was a linearly scaled version of Shannon evenness in our data (Table 1). However, the highest bobwhite populations were associated with the lowest Shannon diversity.

The differences among results reported above probably reflect, to some extent, differences in approaches and interpretations among studies. Brady et al. (1993, 1998) and Roseberry and Sudkamp (1998) modeled over large areas (counties, breeding-bird survey routes, major land resource areas), whereas we worked with 200-ha, circular areas. The identification and mapping of land cover classes involves some subjectivity that could lead to different results among studies. Finally, the influence of a particular land-cover class depends on the context within which it occurs (Mankin and Warner 1999), context meaning the type and arrangement of other land-cover classes relative to the class of interest. Thus, it is possible for a given land-cover class to have variable effects on bobwhite populations, depending on

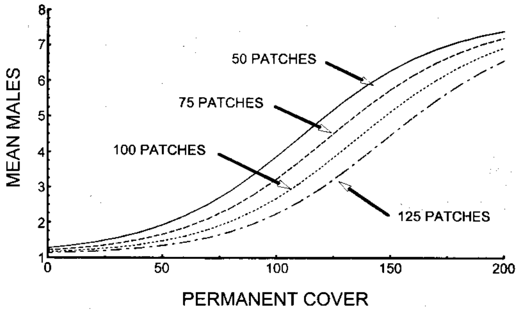

Fig. 6. Response of calling male bobwhites to the quantity of permanent native cover (brushy prairie plus native prairie) and the number of habitat patches on 78 sites in central and western Oklahoma, USA, 1998 and 1999.

where it occurs. The context of habitat patches and juxtaposition could have influenced the results of different studies. Wildlife science needs theory to deal with contexts because the absence of such theory will surely continue to generate confusion.

Management Theory

We conclude with observations on our results relative to the law of dispersion, the patchwork agriculture model of bobwhite abundance, and the space–time hypothesis. Although more woody edge may predict higher bobwhite populations in some settings (Roseberry and Sudkamp 1998), our results provided an empirical counter instance to the law of dispersion as formulated by Leopold (1933:132). This outcome was not surprising because edge has been shown to be a special circumstance within the more general outlook of usable space in time (Guthery 1997). The law of dispersion breaks down when edge is meaningless (of no biological value) or redundant (Guthery and Bingham 1992). Empirically, Hanson and Miller (1961) documented a counter instance to the law of dispersion (adding edge had no effect on bobwhite abundance). The presence of edge is known to be damaging to ruffed grouse (*Bonasa umbellus*; Gullion 1984), nesting birds (Hartley and Hunter 1998), certain amphibians (Demaynadier and Hunter 1998), and ring-necked pheasants (*Phasianus colchicus*; Schmitz and Clark 1999). Leopold's (1933:132) law of dispersion should no longer be considered a management canon because it has been repeatedly disproved. One valid counter-instance is all that is required to destroy a scientific precept (Feynman 1998:16). The law can be resurrected only if other scientists can demonstrate that the counter instances observed, both theoretical and empirical, are invalid.

The highest calling-male populations we observed occurred in the absence of cropland agriculture, contrary to Leopold's (1933:307) patchwork agriculture model of bobwhite abundance. Our results, however, do not clearly refute the patchwork model because none of our study sites provided archetypal patchwork settings. We suggest that patchwork agriculture is perhaps best considered a sufficient but not a necessary condition for high populations of bobwhites. In fact, Leopold (1933:59) reported excellent bobwhite densities (>5/ha) on extensive areas of rangeland in southern Texas, and these findings have been verified subsequently (Guthery 2000). Somewhat ironically, Leopold (1933:52) also reported that bobwhite density rarely exceeded 2.5/ha in the heyday of patchwork agriculture in the Midwest; i.e., he reported higher densities in areas without rather than with patchwork agriculture.

The space–time hypothesis, which originated with the thinking of Stoddard (1931:374), Leopold (1933:52), and Errington and Hamerstrom (1936:434), was formalized by Guthery (1997, 1999). This hypothesis states that bobwhite abundance on an area is a nondecreasing function of the quantity of usable space in time, given sufficient space for population viability and an upper limit on density (Guthery 1996, 1997). Usable space is defined as habitat compatible with the physical, physiological, and behavioral adaptations of bobwhites (Guthery 1997). The positive relation between brushy prairie (permanent cover available at all times) and the call index (Fig. 3E) and between brushy prairie plus native prairie and the call index (Fig. 6) was consistent with the space–time hypothesis. However, usable space in time was not a particularly strong correlate of the call-count index because a large portion of the variation in this index (>70%) remained unexplained by this variable.

We recognize that abundance may be a misleading indicator of habitat quality (Van Horne 1983). For example, a dense but declining population may occupy substandard habitat relative to a sparse but stable or increasing population. Abundance must be interpreted relative to the likelihood of population persistence as governed by survival and reproduction rates. We point out, however, that abundance (crude density) may be an excellent indicator of habitat quality in the sense that Van Horne (1983) implied (quality of an area). In other words, Van Horne did not assert that density is a misleading indicator, only that it could be.

Taylor et al. (1999) addressed fitness (survival) issues relative to the space–time hypothesis. Their results were ambiguous regarding the space–time hypothesis versus the habitat quality hypothesis, which presumes that habitat quality exists and governs fitness. They incorrectly argued that the space–time hypothesis requires constant survival rates, given latitude. This argument is impossible under the theory of natural selection. Rather, Guthery (1997) argued that mean survival and production rates converge to similar values on areas with weather catastrophes of similar pattern, frequency, and severity. Convergence to a constant mean does not preclude variation among individuals and times.

MANAGEMENT IMPLICATIONS

Bobwhite managers should be skeptical of the law of dispersion and the patchwork agriculture model of bobwhite abundance because these management precepts either do not hold under scrutiny (dispersion) or are unnecessary conditions for high densities of bobwhites (patchwork agriculture). To foster the abundance of bobwhites on farms and ranches with low populations in Oklahoma and areas within similar vegetation provinces, applied ecologists should consider reducing the amount of mature woodland or cropland or both. These land-cover classes should be replaced with brushy prairie or early-successional woodland. Much flexibility exists in the composition and arrangement of land-cover classes that leads to high populations, given that the cover classes tend towards permanency. Small to large amounts of native prairie (25–50%) and small amounts of introduced grasses and cropland (<10%) do not appear detrimental. Seed-bearing agricultural crops need not be present for high populations of bobwhites.

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