RELATIVE ABUNDANCE OF BOBWHITES IN RELATION TO WEATHER AND LAND USE

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Abstract: Weather and land use are important factors influencing the population dynamics of northern bobwhites *(Colinus virginianus)* in Texas and elsewhere. Using an artificial neural network, we studied the effects of these factors on an index of bobwhite abundance (hereafter, index) in 6 ecoregions in Texas. We used roadside-count data collected by the Texas Parks and Wildlife Department (TPWD) during 1978-1997. Weather variables were June, July, and August mean maximum temperatures, and winter (Dec-Feb), spring (Mar–May), summer (Jun-Aug), and fall (Sep-Nov) rainfall. We also included the proportion of county area in cultivation, the number of livestock per hectare of noncultivated land, and the previous year's bobwhite count in the analyses. The data were partitioned into training and validation data sets prior to analyses. The neural model explained 65% of the variation in the training data ($n = 72$) and 61% of the variation in the validation data ($n = 17$). The most important variables contributing to network predictions were July temperature, fall rainfall, cattle density, and the previous year's bobwhite count. State-level simulation results indicated that the bobwhite index decreased with increasing June temperature and livestock density. The bobwhite index increased with July and August temperature, fall rainfall, and the previous year's bobwhite count. Bobwhite abundance increased with the proportion of county area in cultivation up to approximately 20% cultivation and then declined. Winter, spring, and summer rainfall had little effect on the bobwhite index. Although many relationships appeared approximately linear or were decelerating, proportion of county area in cultivation and livestock density on noncultivated land showed strongly curvilinear responses. Therefore, cultivation up to approximately 20% of county area was beneficial, but the benefits disappeared as cultivation increased beyond this level. Further, at low livestock densities, between 0.15 and 0.40 head/ha, small increases in head/ha resulted in a decrease in the bobwhite index of 156.4%/head/ha. The results also indicated that a potential bias might exist in the survey protocol resulting in artificially inflated counts under some weather conditions.

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The northern bobwhite (hereafter, bobwhite) is an important game species in many parts of its range. Although declines have been noted since at least the 1880s (Errington and Hamerstrom 1936), bobwhite abundance typically follows a boom-or-bust pattern, with considerable variation among years (Stoddard 1931, Stanford 1972, Roseberry and Klimstra 1984:130). Possible factors influencing the long-term trends in bobwhite abundance include climate change, habitat loss, and land-use change (Edwards 1972, Klimstra 1982, Brady et al. 1993, Schemnitz 1993, Rotenberry 1998). Although typically regarded as compensatory, harvest may be an additive source of mortality in years of low production (Pollock et al. 1989, Johnson and Braun 1999, Guthery et al. 2000). Before harvest and habitat management can be effective at maintaining harvestable populations, an understanding of the factors influencing bobwhite abundance that are not amenable to management, such as weather, is required. It is against the backdrop of weather effects that habitat and harvest management must operate.

Although catastrophes such as blizzards and droughts can devastate bobwhite populations (Errington and Hamerstrom 1936, Leopold 1937, Roseberry 1964), noncatastrophic weather events may be important determinants of bobwhite abundance (Edwards 1972, Stanford 1972, Roseberry and Klimstra 1984, Giuliano and Lutz 1993). In arid and semiarid regions, precipitation is an important component of avian survival and reproduction (Newton 1998:288). However, temperature also can affect bobwhite production (Leopold 1933, Robinson and Baker 1955,

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Speake and Haugen 1960, Stanford 1972, Guthery et al. 2001). Precipitation and temperature can act directly through increased mortality (Leopold 1931, Sumner 1935, Newton 1998), changes in the length of the breeding season (Klimstra and Roseberry 1975, Guthery et al. 1988), and reduction in reproductive effort (Murray 1958; Guthery et al. 1988,2001); or indirectly through its effects on habitat and food availability (Swank and Gallizioli 1954, Sowls 1960, Newton 1998). Further, weather effects can interact with habitat conditions to influence bobwhite abundance. For example, Rice et al. (1993) modeled bobwhite abundance as a function of habitat variables and weather conditions. Although the model including only weather effects accounted for more variation than the habitat-only model, a combined model accounted for almost twice as much variation as either separate model (Rice et al. 1993). Similarly, better site quality ameliorated the effects of drought on bobwhite density compared with poorer quality sites (Webb and Guthery 1982).

Recent work by Bridges et al. (2001) in Texas showed that, although 12-month precipitation was positively correlated with bobwhite abundance in the South Texas Plains, the 12-month Palmer Modified Drought Index (PMDI) was more strongly correlated with bobwhite abundance. These authors also reported that monthly PMDIs were positively correlated with bobwhite abundance in the Cross Timbers and Prairies (Nov–Feb, $r_S \geq 0.57$), Edwards Plateau (Sep–Nov, $r_S \geq 0.59$), Rolling Plains (Sep–Feb, Apr, Jun; $r_S \geq 0.56$), and South Texas Plains (Oct–Jul, $r_S \geq 0.56$), whereas raw precipitation was positively correlated with bobwhite abundance only in the South Texas Plains. Although the PMDI is a composite index containing more information than precipitation alone, Bridges et al. (2001) did not explicitly represent temperature (although temperature is used to calculate the PMDI), land use, stocking density, or broodstock. Further, as a composite index, the separate effects of individual components (e.g., temperature and precipitation) cannot be assessed, Although Bridges et al. (2001) demonstrated the importance of weather to bobwhite population dynamics, an analysis explicitly considering the separate effects of rainfall, temperature, land use, stocking density, and broodstock could be useful to bobwhite managers. For example, Guthery et al. (2001) reported heat loads in southern Texas sufficient to alter bobwhite breeding behavior and physiology. They found that during the hotter year of a 2-year study, heat loads were sufficient to reduce calling activity of male bobwhites by approximately 84%. Therefore, it appears that temperature, as represented by heat loads, might play an important role in bobwhite production. Furthermore, Guthery (1999) suggested that any number of habitat configurations could result in the maximization of demographic potential, as long as these configurations permitted fully saturated habitat space–time (Guthery 1997). That is, the exact configuration of the habitat patch is not important as long as the configuration meets the bobwhite's habitat requirements. Several authors have attempted to determine such optimal habitat conditions for bobwhites (e.g., Edminster 1954, Schroeder 1985). Spears et al. (1993), for example, found that habitat suitability varied with land productivity, such that earlier successional stages were more suitable for bobwhites in more productive areas and later successional stages were more suitable in less productive areas.

There are 2 additional reasons why the nonlinear approach described below should add to our knowledge regarding how weather influences bobwhite abundance. First, although correlative analyses, such as those of Bridges et al. (2001) and most other published studies, can indicate general relationships among predictor and response variables, they are not necessarily conducive to determining the functional relationships among the variables. That is, correlation coefficients may indicate a positive response to increasing values of the other variable, but the lack of a strong correlation may not indicate a lack of a relationship between the variables. Second, nonlinear biological responses to environmental variation sometimes can result in spurious correlations depending on the functional response of the biological system and the pattern of the environmental variation (Laasko et al. 2001). For example, if bobwhite abundance varies in a symmetric, unimodal fashion with temperature, then, depending on the observed range of temperatures with respect to the abundance-response function, there may be positive, negative, or no relation apparent from the correlations, even when temperature is a strong forcing variable for bobwhite abundance.

For these reasons, we investigated the relationship between bobwhite abundance in 6 ecoregions in Texas and rainfall, temperature, land use, and broodstock using a nonlinear, neural network algorithm to obtain a more complete understanding of bobwhite population dynamics. We also addressed the relative importance of each variable in determining region-level bobwhite abundance in Texas. We then used simulations to investigate the pattern of bobwhite response to each environmental variable. Finally, we investigated regional patterns of abundance to determine potential limiting factors at the ecoregion level.

METHODS

Neural Network Architecture

We used a 3-layer network architecture and trained neural models using QNet 2000 (Vesta Services, Winnetka, Illinois, USA) backpropagation neural modeling software. The first layer consisted of the input (independent) variables. Our database contained 10 input variables (7 weather, 2 land use, 1 population). To optimize model performance, we experimentally varied the number of neurons between 2 and 10 in a series of models while holding all other training parameters constant. We selected the model that produced output with the highest correlation with actual counts for both the training data and the validation data (see below). The selected model, therefore, provided the best trade-off between predictive power and generalizability. The output layer consisted of a single output node (dependent variable) representing mean bobwhite count/route/ecoregion/year. We trained the networks for 2,000 iterations and used an adaptive learning rate that varied between 0.01 and 0.30. The learning rate determines how fast the network learns by limiting the magnitude of changes to the synaptic weights during training (Smith 1996:88-90). To prevent overtraining, which occurs when the network has learned to predict the data exactly, we stopped training when the decrease in the error began to approach an asymptote.

Database Construction

We obtained bobwhite abundance data from TPWD records for 1978 through 1997. These data were collected annually during the first 2 weeks of August along randomly placed and permanently marked 32.2-km routes (Perez 1998). Routes were traveled at 32 km/hr, and total quail observed was recorded at 1.6-km intervals. We used data from those ecoregions (Gould 1975) where bobwhites were consistently counted during 1978–1997: the Gulf Prairies, Cross Timbers, South Texas Plains, Edwards Plateau, Rolling Plains, and High Plains. Although the database contained data for 156 routes, some were not run every year, so 2,624 route-by-year combinations, of a potential 3,120, were available. Raw counts from all routes within an ecoregion were averaged for each year to produce a composite index (bobwhite count/route/ecoregion/year), resulting in a final sample size of 89 cases. Although this composite index reduced the amount of variation in the abundance data, it is an appropriate level for the analysis of broad-scale weather effects (O'Neill et al. 1986),

We obtained weather data from the National Atmospheric and Oceanic Administration's National Climatic Data Center records (EarthInfo, Boulder, Colorado, USA, 1998) for the weather stations closest to each route's starting point using latitude and longitude coordinates provided by TPWD. We constrained selection to those weather stations with $\geq$ 90% complete data for 1977–1997 and that were within 1° of latitude and longitude. We then averaged the mean maximum temperature in June, July, and August and total winter, spring, summer, and fall rainfall in the same way we did count data.

We also addressed land use in our analyses. We used the proportion of cultivated land and the number of livestock per hectare of noncultivated land in each county in which a survey route was located as land-use indices. We obtained crop and livestock data from the Texas Department of Agricultural Statistics. Cropland was summed for each county and then averaged within each ecoregion for each year. Similarly, livestock densities for each year were averaged within ecoregions. Livestock data were not available for 1988 through 1992 (inclusive), because funding for the livestock statistics program was not available (R. Roark, Texas Agricultural Statistics Service, personal communication). Although the database we used in this analysis did not include 1988 through 1992 as a result, models excluding all livestock data and including these years resulted in qualitatively similar results for the remaining variables. We recognize that this measure of grazing pressure does not account for the temporal distribution and intensity of grazing livestock but should give a relative estimate of grazing pressure among ecoregions. The final independent variable in our analyses was the number of bobwhites counted the previous year averaged for each ecoregion. We included this variable to account for possible density-dependent effects, which also vary spatially.

Table 1. State- and ecosystem-level means for independent variables used to develop a predictive model for northern bobwhite abundance in Texas, USA, 1978–1997.

Variable	Statewide	Ecoregion[a]					
		2	5	6	7	8	9
Maximum temperature (°C)							
Jun	32.9	32.6	32.7	34.0	33.1	32.7	32.6
Jul	35.4	34.4	35.7	36.2	35.6	35.8	34.8
Aug	34.9	34.4	35.7	36.3	35.4	34.8	32.9
Seasonal rainfall (mm)							
Winter	111.4	215.2	133.3	101.2	101.2	74.7	44.3
Spring	193.0	268.2	250.1	177.3	171.1	180.3	115.0
Summer	201.7	289.2	195.4	184.0	168.3	192.3	180.1
Fall	203.3	340.1	241.4	189.1	175.2	158.4	131.4
Cropland[b]	0.15	0.22	0.08	0.1	0.04	0.18	0.28
Livestock density[c]	0.30	0.33	0.35	0.23	0.34	0.23	0.33
Previous year's bobwhite count	14.0	6.0	18.0	22.6	13.0	21.4	3.5

[a] Ecoregions: 2 = Gulf Prairies, 5 = Cross Timbers, 6 = South Texas Plains, 7 = Edwards Plateau, 8 = Rolling Plains, 9 = High Plains.
[b] Mean proportion of county area in cultivation.
[c] Mean head of livestock per hectare of noncultivated land.

We partitioned the data ($n = 89$) into training and validation data sets. We first ranked the data according to mean bobwhite count/ecoregion/year, then systematically selected every fifth record and assigned it to the validation data set. This resulted in a validation data set that was approximately 20% of the total. We did not use a random assignment protocol, because neural networks learn from the data presented to them in the training data set. For this reason, it is necessary that both training and validation data represent the full range of variation in the complete database (Fielding 1999:25-26). Training cases were used to adjust the synaptic weights during the training process. Validation cases were presented to the model during the training process to assess the models performance but were not used to adjust the synaptic weights. Validation cases, therefore, indicated how well the model performed when presented novel data. Although this was not validation in the strict sense (Conroy 1993, Oreskes et al. 1994, Conroy et al. 1995), this method allowed us to assess model performance (Rykiel 1996).

Model Interpretation

Although neural network models often perform well as predictors or discriminators, the nature of their architecture makes the synaptic weights difficult to interpret (Anderson 1995, Lek et al. 1996). There are 2 approaches to overcome this difficulty. The first is to estimate the relevance (Ozesmi and Ozesmi 1999) of each input variable, which assigns an importance value for each input (independent) variable to the model's overall prediction. Relevance is calculated as the sum of squared synaptic weights from 1 input node divided by the sum of squared synaptic weights for all input nodes. Input nodes with larger synaptic weights exert more control over a model's response to a given stimulus.

The second method for dealing with the difficulty in interpretation of the synaptic weights is through simulations (Lek et al. 1996). We used this approach by creating a series of databases that allowed the variable of interest to vary between the maximum and minimum value on record while all other variables were held constant at a mean value for pooled data or individual regions. We also created individual data sets for each variable in the model using the overall database means. These data sets were presented to the trained model, and the model's predictions revealed the nature of response to variation in the variable of interest when all other variables were held constant at mean values. Results report approximate values for the variable of interest obtained from the simulation analysis.

We then presented the trained model with both state- (for only those ecoregions used in these analyses) and ecoregion-level means (Table 1) to determine how ecoregion-level counts varied from state-level counts when conditions were average. The resulting predictions allowed us to evaluate populations in each ecoregion when conditions are average and to compare these predictions with state-level predictions. We further investigated the relationship between bobwhite abundance and the variables in our model by evaluating our simulation results with regard to

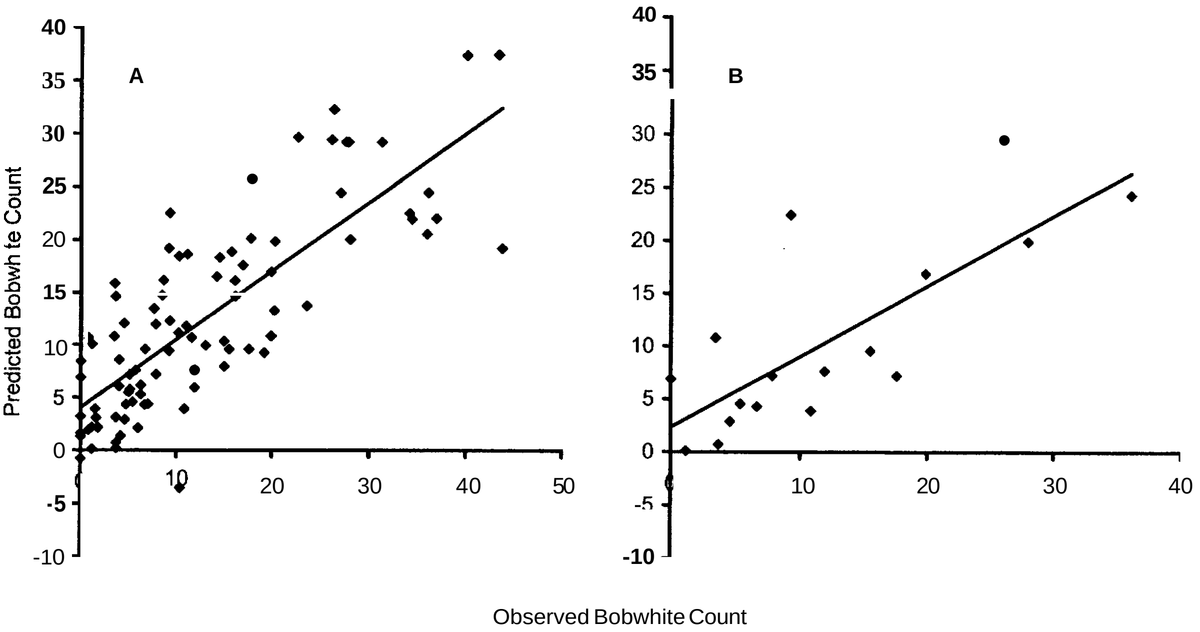

Fig. 1. Predicted versus observed northern bobwhite counts recorded by Texas Parks and Wildlife Department biologists during annual Aug surveys (1978–1997) for training data (A) and validation data (B) using a 4-neuron neural network. The trend line indicates the linear relationship between predicted and observed counts.

mean (i.e., average) conditions. We did this by plotting the mean value for each variable on the graph of its simulation results, allowing us to determine possible predictive factors for bobwhite abundance in the region. For example, if the mean value for a particular variable falls below the peak in the bobwhite index, then relative abundance would be higher for any greater value for that variable, Therefore, such a variable might be constraining, or limiting, relative abundance.

RESULTS

A 4-neuron model was optimal for the overall data set and explained 65% of the variation in the training data (Fig. 1A) and 61% of the variation in the validation data (Fig. 1B). The variables most important to the network's predictions (relevance >l0%) were July temperature, fall rainfall, livestock density on noncultivated land, and the previous year's bobwhite count (Table 2). The proportion of county area in cultivation also was important, but its relevance score was below (9.3%; Table 2) our arbitrary 10% cutoff point. The remaining variables also influenced the index of abundance, but to a lesser extent (see Discussion). We, therefore, report the results for all simulations below, but focus discussion on the most relevant variables.

The index declined linearly with increasing mean maximum June temperature (Fig. 2A). Given that all other conditions were average, the network predicted counts of 21 bobwhites when maximum June temperatures averaged 30 °C. However, at an average of 37 °C, only 10 bobwhites would be counted. This translated into a decline of 1.6 bobwhites/°C increase in mean maximum June temperature. In contrast, the bobwhite index increased linearly with increasing

Table 2. Relevance (importance) of input variables in a 4-neuron neural model developed to predict the abundance of northern bobwhites in Texas, USA, based on data collected during 1978–1997. Relevance is calculated as the sum of the squared weight of the variable of interest divided by the sum of squared weights for all inputs. The higher the relevance score, the more the variable contributes to the model's predictions and, therefore, gives the relative importance of each variable.

Input variable	Relevance
Maximum temperature (°C)	
Jun	8.4
Jul	15.7
Aug	7.6
Seasonal rainfall (mm)	
Winter	8.1
Spring	5.9
Summer	3.0
Fall	15.9
Cropland[a]	9.3
Livestock density[b]	11.9
Previous year's bobwhite count	14.4

[a] Mean proportion of county area in cultivation.

[b] Mean head of livestock per hectare of noncultivated land.

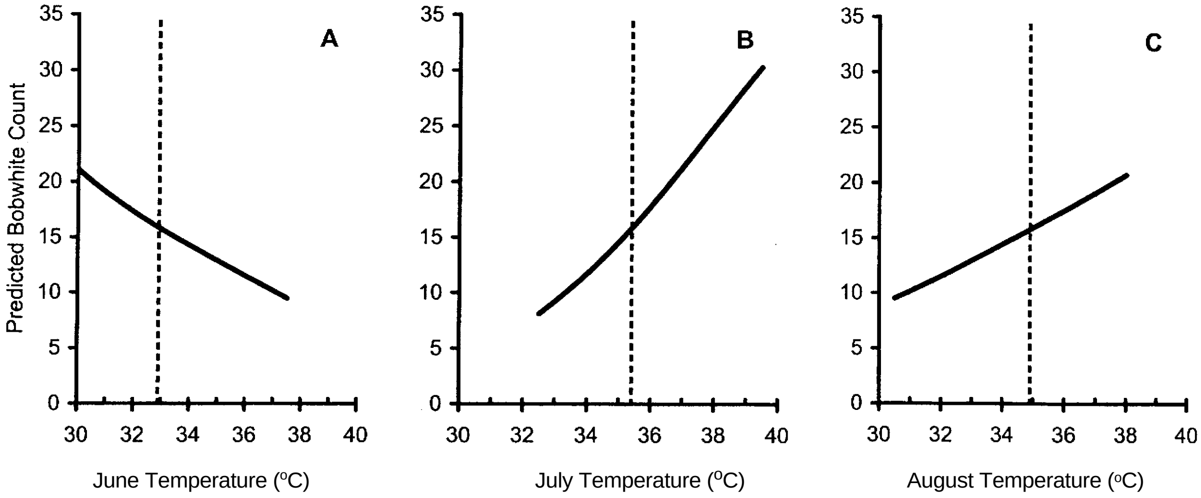

Fig. 2. Predicted northern bobwhite counts from simulation analyses of the effects of Jun (A), Jul (B), and Aug (C) mean maximum temperature (°C) generated from the trained neural model using a data set in which the independent variable of interest varies between its minimum and maximum, and all other independent variables are held constant at their statewide mean (Table 1). Dashed vertical lines indicate the mean value of the independent variable. The same scale was used for each plot's Y-axis to provide information on sensitivity.

mean maximum July temperature (Fig. 2B). Predicted counts increased by 3.1 bobwhites/°C increase in July temperature, with peak abundance of 30 bobwhites at 40°C. Increases in mean maximum August temperature were also associated with linear increases in the index (Fig. 2C). At August temperatures of 31°C, the bobwhite index was 10 bobwhites, but reached a maximum of 21 bobwhites at 38 °C. Predicted counts increased by 1.4 bobwhites/°C increase in August temperature.

The network predicted that increases in winter rainfall were nonlinearly related to the bobwhite index, although the effect was slight (Fig. 3A). The bobwhite index was unresponsive to either spring (Fig. 3B) or summer (Fig. 3C) rainfall in our simulations. Increasing fall rainfall resulted in increased bobwhite counts, but the relationship was slightly decelerating (Fig. 3D). When fall rainfall was 27 mm, the bobwhite index was predicted to be 8. When fall rainfall reached 500 mm, the index was predicted to be 24.

The bobwhite index varied curvilinearly with the proportion of county area in cultivation (Fig. 4A), and increased by 25% with increasing cultivation until 20% of county area was under plow, at which point predictions peaked at 16 bobwhites. Further increases in cultivation reduced the bobwhite index 43.8%, to a low of 9, at 48% of county area in cultivation. In contrast, increases in livestock density on noncultivated land were followed by declines in the index (Fig. 4B). The bobwhite index dropped rapidly from 23 at 0.15 head/ha to 14 bobwhites at 0.4 head/ha. This represents a decline of 39.1% for a 0.25 head/ha increase in livestock density or a decline of 156.4%/head/ha increase in livestock density. Declines thereafter were less dramatic, reaching a low of 7 bobwhites when livestock density reached 1.2 head/ha. The index in the current year increased with increases in the previous year's count, but at a slightly decelerating rate (Fig. 4C), indicating potential density dependence. When the previous year's count was 0, our model predicted a current-year count of 10 bobwhites. Current-year counts were highest at 30 bobwhites when the previous year's count was 66 bobwhites.

Predictions generated using state- and ecoregion-level means as independent (input) variables indicated that, if all conditions were at their statewide average, relative abundance would be expected to be 16 bobwhites/route/ecoregion. Because of the range of variation in weather conditions across Texas, this number can serve as a benchmark for comparing ecosystem responses. Based on average conditions in the Gulf Prairies, the network predicted 3 bobwhites/route. Similarly, average conditions in each remaining ecoregion produced predictions of 20 bobwhites/route in the Cross Timbers, 19/route in the South Texas Plains, 11/route in the Edwards Plateau, 20/route in the Rolling Plains, and 5/route in the High Plains. Predicted counts based on ecoregion-level means were smaller than predicted counts based on the statewide

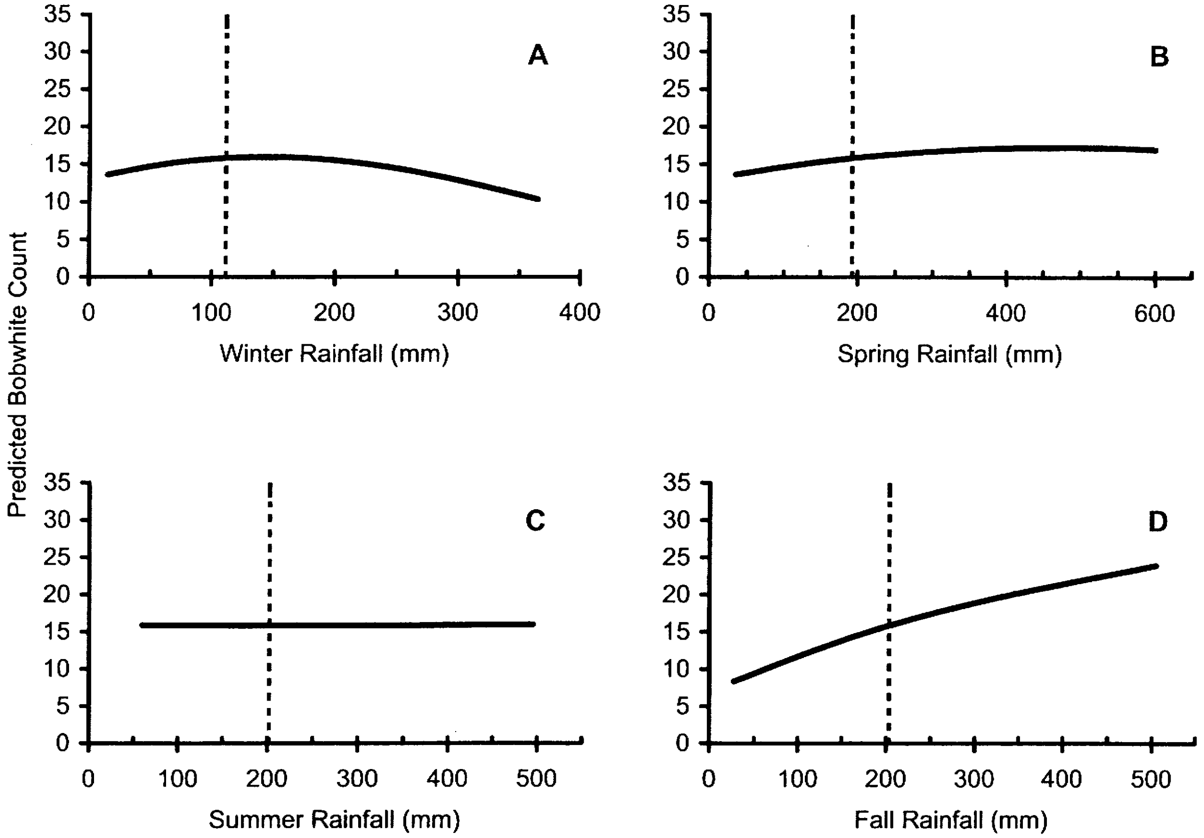

Fig. 3. Predicted northern bobwhite counts from simulation analyses of the effects of winter (A), spring (B), summer (C), and fall (D) rainfall (mm) generated from the trained neural model using a data set in which the independent variable of interest varies between its minimum and maximum, and all other variables are held constant at their statewide mean (Table 1). Dashed vertical lines indicate the mean value of the independent variable. The same scale was used for each plot's Y-axis to provide information on sensitivity.

means in the Gulf Prairies, Edwards Plateau, and the High Plains. Comparing means for the 5 most important variables in the model (Tables 1, 2) between these ecoregions and the state level does not indicate any consistently different trends, except that the mean of the previous year's counts were lower in these 3 ecoregions than the statewide mean (Table 1). Likewise, the mean previous year's count for the Cross Timbers, South Texas Plains, and the Rolling Plains, where predicted counts were larger than the count based on the statewide means, were larger than the statewide mean previous year's count.

Our analysis of potential limiting factors indicated that several environmental variables might be limiting population growth at the state level. For instance, simulation results indicated that abundance might be limited by fall rainfall (Fig. 3D). If average years are frequent, then the 203.3 mm of rainfall in the average autumn is below the amount at which the bobwhite index achieved maximum level in our results. In contrast, there appears to be excessive grazing, as measured by livestock density/ha of noncultivated land (Fig. 4B). The index was greatest when livestock density was less than the statewide mean of 0.30 head/ha. Overall, current levels of cultivation in Texas appear to be appropriate for bobwhites (Fig. 4B), since the statewide mean (15% of county area) is near the density at which the bobwhite index peaked (but see Discussion).

DISCUSSION

Although networks with more neurons tended to produce slightly better agreement between predictions and observations, the 4-neuron network used in this analysis contained fewer parameters while still accurately predicting an index of bobwhite abundance at an ecoregion level in Texas, based on weather and broad-scale, land-use variables. Further, our training procedure ensured that the network we obtained made the best compromise between bias and variance (Lek et al. 2000).

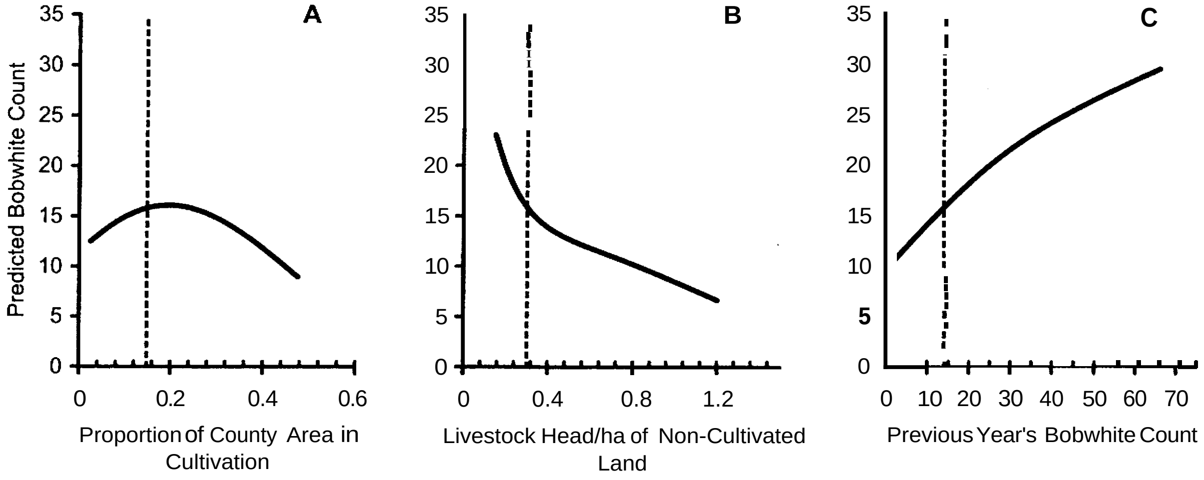

Fig. 4. Predicted northern bobwhite counts from simulation analyses of the effect of the proportion of county area in cultivation (A), head of livestock per hectare of noncultivated land (B), and previous year's bobwhite count (C). Predictions were generated from the trained neural model using a data set in which the independent variable of interest varies between its minimum and maximum, and all other independent variables are held constant at their statewide mean (Table 1). Dashed vertical lines indicate the mean value of the independent variable of interest. The same scale was used for each plot's Y-axis to provide information on sensitivity.

July temperature was an important determinant of the bobwhite index in our model. These results are contrary to expectations based on previous work. For example, age ratios of Gambel's quail *(Callipepla gambelii)* decreased with increasing July temperature in Arizona (Heffelfinger et al. 1999). Similarly, in Oklahoma, bobwhite abundance declined with increasing July temperature (Lusk et al. 2002). Both of these studies used the same analytical technique that we employed in our analysis, so differences in results do not relate to differences in techniques. It is possible that the differences in results between the Gambel's quail study and our study result from differences in the ecologies of Gambel's quail and bobwhites. Gambel's quail are native to the arid Southwest (Kaufman 1996) and, as such, might respond differently to weather than bobwhites. The differences between the results of the current study and Oklahoma study are more difficult to explain, but may reflect latitudinal differences in weather conditions and possibly land use.

One hypothesis that may explain our contradictory results is that bobwhites may congregate along roadsides during hot, dry conditions in which vegetation may be more lush, green, and ungrazed, similar to conditions in more central parts of their range. Because detection and behavior are affected by weather (Roseberry and Klimstra 1984), conditions both before and during roadside counts can affect the number of bobwhites counted, and, therefore, the number of bobwhites predicted by the model. For example, Guthery et al. (2001) found that calling behavior of bobwhite males was coincident with the thermal environment measured on different days. Therefore, detectability, and not just abundance, may vary in time due to environmental conditions at different temporal scales. Temperatures >35 °C stimulated heat dissipative behaviors in captive bobwhites (Spiers et al. 1983), and the range of observed values in our data set bounded this landmark temperature. Roadsides may provide a thermal refuge for bobwhites along the less intensely grazed verges. This may occur because cattle grazing may exacerbate the impacts of drought on primary production in grazed pastures, resulting in greater apparent stocking rate (Fuhlendorf and Smeins 1997). Conversely, if high temperatures are accompanied by low amounts of rainfall (i.e., drought), then vegetation density along roadsides may decrease, rendering bobwhites more detectable. However, drought had little influence on the composition of ungrazed pastures in the Edwards Plateau (Fuhlendorf and Smeins 1997) although rainfall influenced both plant basal area and total plant density (Fuhlendorf et al. 2001). These 2 hypotheses are not mutually exclusive and other hypotheses are possible. Although vegetation along roadsides can be sparse in drought years, it may still provide the only cover available, thus drawing bobwhites to the roadsides. Immediately after a rain shower, detection may increase as bobwhites move out onto the roadway to dry. It also is possible that the observed response in the bobwhite index to July temperature was an artifact of the data we used and, therefore, the predicted relationship might be spurious (Anderson et al. 2001). Further research should be directed at testing the above hypotheses to determine their validity and to assuage any concerns of state natural resource agencies that may conduct similar types of surveys.

Although spring and summer, and to a lesser extent winter, rainfall had little effect on model predictions, fall rainfall was an important determinant of the relative abundance of bobwhites in Texas. The strongly positive effect of fall rainfall was consistent with our prior expectations based on previous research. In particular, Bridges et al. (2001) reported a positive correlation between PMDIs for fall months and the number of bobwhites counted during the next August in the Edwards Plateau, Rolling Plains, and the South Texas Plains. Similarly, age ratios for Gambel's quail in Arizona responded positively to variation in October–November (fall) rainfall, but predicted increases were only 0.5-0.6 juveniles/adult/mm rainfall (Heffelfinger et al. 1999).

Relative abundance declined with increasing livestock density in our model. These declines might have resulted not only from higher livestock densities per se but also from changes in land use and cover associated with these densities. Grazing can reduce the structural diversity of rangelands (Archer and Smeins 1991, Fleischner 1994), can alter the competitive interactions among the plant species leading to woody encroachment (Archer and Smeins 1991), and can alter the amount and effectiveness of thermal cover (Barnes et al. 1991). A livestock density of <0.2 head/ha (>5 ha/head) indicated native pasture in a primarily rangeland setting; conversely, a livestock density of 1.2 head/ha (0.8 ha/head) indicated introduced pasture in regions of higher rainfall. Although relative bobwhite abundance is positively correlated with rangeland within their historic range (Brady et al. 1998), heavy grazing over the long term lowers the successional status of the vegetation. Specifically, heavy grazing in the Edwards Plateau resulted in decreases in native bunchgrasses and increases in shorter sodgrasses (Fuhlendorf and Smeins 1997). In semiarid environments, bobwhites on rangelands tend to be more abundant in higher seres than in lower seres (Spears et al. 1993). Rangelands in south Texas, for example, can support bobwhite densities >5 bobwhites/ha (Leopold 1933:59, Guthery 2000:19) on native pasture. Conversely, introduced pastures, often planted to exotic grasses and managed intensively, usually provide wholly unsuitable habitat for bobwhites. Further, because nest predation rates tend to be lower in areas with more ground cover (Cooper and Ginnett 2000), one might expect higher stocking densities on rangelands to be associated with higher nest predation rates, thus reducing production and the subsequent count during the August survey.

Our model predicted that the current year's relative abundance increases at a decelerating rate with increasing previous year's abundance, suggesting a density-dependent response. Oklahoma bobwhites also exhibited an apparent density-dependent response, but predictions of current year's relative abundance declined with increases in previous year's index >25 bobwhites (Lusk et al. 2002). Similarly, Roseberry and Klimstra (1984:96) reported a negative correlation between production (measured as percent summer gain) and the previous year's breeding population size in Illinois. They suggested that hunting mortality maintained the study population below levels where density effects could impact bobwhite production (Roseberry and Klimstra 1984:102). Therefore, hunting might mask density-dependent patterns of production in heavily exploited populations. Further research is needed to determine whether harvest pressure is sufficient in Texas to account for the different results, or whether other factors are involved.

Our analysis indicated that average conditions were sufficient within each ecoregion to support bobwhite populations. However, predicted indices in the Gulf Prairies and the High Plains were below 10 bobwhites/route. This indicates that average weather and land-use conditions in these ecoregions, over the period of this study, were less optimal for bobwhites than other parts of Texas. An analysis of mean weather conditions in these ecoregions (Table 1), with respect to our simulation results, indicated that for the High Plains, bobwhite abundance might be limited by low winter and fall rainfall (44.3 mm and 131.4 mm, respectively). Reasons for low abundance in the Gulf Prairie, based on ecoregion means, are less clear.

Although our results indicated that mean statewide levels of cultivation appeared optimal in Texas, agricultural development is not uniform across the state (Table 1) and, therefore, suitability will depend on the regional context. That is, ecoregion level means for cultivation will differ from the statewide mean and from the optimal level of cultivation as indicated by our model. Further, both the statewide and regional means do not reflect the spatial distribution of the cultivated lands in the landscape. Therefore, predictions based on these means must be interpreted with some caution.

MANAGEMENT IMPLICATIONS

Our results have 2 implications for management. First, we identified a potential bias inherent to the roadside quail survey conducted by TPWD. The increased counts associated with increased maximum temperatures in July are inconsistent with biological expectations. This apparent paradox may be explainable by simple processes of bobwhite behavior and visibility. Alternatively, it could also be an artifact of the data (Anderson et al. 2001). If not, it could lead to overestimates of relative abundance during hot July days. One might question whether the increased variability resulting from such a bias would be important to state wildlife agencies considering all the other inconsistencies already inherent in such surveys (e.g., changing land use along routes, different observers on a given route, or changing observer skill over time). We maintain, however, that it is important for managers to realize such a bias might exist. For example, one might want to temper predictions of bobwhite abundance during the next hunting season after a particularly hot summer. Further research seems warranted to test the hypotheses regarding these observed and paradoxical responses, so that we can garner a more reliable understanding of bobwhite–weather relationships.

The second implication of our results to management is at the statewide and ecoregion level. Since weather is beyond the control of the resource manager, management efforts must focus on land-use practices. We included 2 relatively broad-scale measures of land use in our model. Simulation results provided insights into the responses of the bobwhite index to variation in land use when weather patterns were controlled. Patterns in long-term data indicated that region-wide reductions in livestock density result in commensurate region-wide increases in the bobwhite index. Further, bobwhite relative abundance was greatest when the amount of cultivation was 20% of county area, and bobwhites generally declined across the landscape as cultivation approached 50% of county area. Therefore, reducing grazing intensity and maintaining low levels of cultivation appear to be appropriate management options for bobwhite populations in Texas.

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