ELSEVIER

Ecological Modelling 146 (2001) 3–15

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

Northern bobwhite (*Colinus virginianus*) abundance in relation to yearly weather and long-term climate patterns

Jeffrey J. Lusk [a,*], Fred S. Guthery [a], Stephen J. DeMaso [b,1]

[a] *Department of Forestry, 008 C Agriculture Hall, Oklahoma State University, Stillwater, OK 74078, USA*
[b] *Oklahoma Department of Wildlife Conservation, Oklahoma City, OK 73105, USA*

Abstract

We used a multilayered, backpropagation neural network to investigate the relative effects of yearly weather and long-term climate patterns on the abundance of northern bobwhites (*Colinus virginianus*: hereafter, bobwhite) in Oklahoma, USA. Bobwhite populations have been declining for several decades across the United States, and predicted global climate change might accelerate the rate of decline. We were interested in whether bobwhite abundance was more responsive to yearly precipitation and temperature, or to annual deviations from long-term mean climate patterns. We used roadside count data collected over a 6 year period (1991–1997) by the Oklahoma Department of Wildlife Conservation as a measure of bobwhite abundance. We standardized quail counts among counties by calculating the standard normal deviate for each county. Weather data were obtained from weather stations closest to the roadside-count route. We had 280 training cases and 68 test-validation cases. Two data sets were constructed: one using yearly weather data (actual rainfall and temperature) and the second using annual deviations from long-term mean values. We conducted simulation analyses to determine the nature of the relationship between each dependent variable and the standardized bobwhite counts. A neural network with eight neurons was most efficient for the yearly weather data, accounting for 25% of the variation in the training data. The adjusted sum-of-squares for this model was 2.42. A four-neuron network was selected for the deviation-from-normal data set, accounting for 23% of the variation in the training data. The adjusted sum-of-squares for the deviation model was 1.44, indicating it performed better than the model for yearly weather patterns. Deviation from long-term mean July and August temperatures combined contributed 31.5% to the climate network's predictions, and deviations from mean winter, spring, and summer precipitation combined contributed 42.8% to the network's predictions. As July temperature increased over the long-term mean, the number of bobwhites counted increased over the route mean, but the relationship decelerated at high July temperatures. Predicted increases in bobwhites counted were highest when August temperatures were below the mean and decreased rapidly for all temperatures greater than the mean. Predicted bobwhite counts increased asymptotically as winter rain increased over the long-term mean, but were greatest at mean spring-rainfall amounts and at below average amounts of summer rainfall. We conclude that the absolute changes in yearly weather pattern predicted by some global change models will not have as great an impact on bobwhite abundance as will the magnitude of the deviations of these values from the climate bobwhites are adapted to in this portion of their range. © 2001 Elsevier Science B.V. All rights reserved.

---

[*] Corresponding author. Tel.: +1-405-7448047.

E-mail address: luskj@okstate.edu (J.J. Lusk).

[1] Present address: Wildlife Division, Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, TX 78744, USA.

PII: S0304-3800(01)00292-7

Keywords: Artificial neural networks; Climate adaptation; *Colinus virginianus*; Global warming; Northern bobwhites; Population abundance; Weather patterns

1. Introduction

Global climate-change scenarios predict an increase in the mean annual temperature of 1–4°C by the middle of next century (Peters, 1992; Schneider, 1993). Concurrent with these changes, overall climate patterns will shift. Global climate change may result in changes in frequency and timing of rainfall, increases in the frequency of catastrophic weather events (Houghton et al., 1990), and changes in diurnal temperature patterns (Easterling et al., 1997). Regional patterns in climate change also may vary (LaRoe, 1991). For the Great Plains, climate change is predicted to bring an overall decrease in precipitation, increased evapotranspiration, and mean annual temperatures greater than the predicted global mean (LaRoe, 1991).

The impacts of these climate changes on wildlife species may result either from direct impacts of weather events or through an inability of particular species to adapt to rapid changes in climate patterns. First, wildlife species may not be able to physiologically tolerate certain weather conditions (Dawson, 1992; Dunham, 1993). The increased temperatures may be lethal to some species that exist near the upper limits of their thermal tolerance (Tracy, 1992). Further, there may be direct losses due to flooding, blizzards, drought, and heavy rains (weather events) in certain areas. As they increase in frequency, these catastrophic factors could become significant sources of mortality. Alternatively, wildlife species may not be able to adapt their life-history strategies, breeding phenology, or behaviors rapidly enough to keep pace with climate change (Rubenstein, 1992). In some species, the timing of breeding is tied to peak food availability. Changes in rainfall seasonality could shift peak food abundance outside the breeding and rearing periods. An inability to track such shifts would result in reduced production. In some cases, climate changes may have positive effects for production by increasing the length of the breeding season (Brown et al., 1999).

Although both effects of weather and climate patterns likely play a role in the abundances of species within their ranges, an understanding of the relative strengths of each factor may help managers better prepare for the coming changes to the biosphere. We investigated the effects of climate and weather on population abundances of northern bobwhites in Oklahoma using artificial neural networks. We also employed simulation analyses to explore the effects of individual weather and climate variables on bobwhite abundance and to help evaluate network predictions. Specifically, we attempted to determine whether annual indices of bobwhite abundance were more sensitive to weather conditions within years or to the deviations of these weather patterns from long-term trends. We accomplished this using a neural network modeling technique (Smith, 1996; Haykin, 1999). This modeling technique allows for non-linear and linear relationships between predictor and response variables without a priori specification of the form of the relationship. Further, because it adapts and learns from the data presented to it, it typically out performs traditional statistical modeling techniques (Smith, 1996).

2. Methods

2.1. Northern bobwhites

The northern bobwhite is a quail of the order *Galliformes*, family *Phasianidae* (Gill, 1995). The bobwhite ranges over much of the southeastern and central United States, with populations as far north as Wisconsin (Kaufman, 1996). Typical habitat characteristics for bobwhites include grasslands, crop fields, and brushy cover (Edminster, 1954), but the optimal configurations and proportions of habitat components for bobwhites can vary widely over most of their range (Guthery, 1999).

Annual indices of bobwhite abundance estimated using data from the North American Breeding Bird Survey (Bystrak, 1981) indicate a consistent long-term decline of 2.4% per year (Church et al., 1993; Sauer et al., 1997). However, the rate of decline accelerated between 1982 and 1991 to 3.5% per year (Church et al., 1993). In Oklahoma, the long-term rate of decline has not been as severe, averaging only 0.20% per year (Sauer et al., 1997), but during the period between 1993 and 1996, the rate of decline in Oklahoma accelerated to 7.36% per year (Sauer et al., 1997).

2.2. Abundance indices

We used roadside count data collected by the Oklahoma Department of Wildlife Conservation (ODWC) in each county in Oklahoma, excluding Oklahoma and Tulsa counties, which had large urban areas (Peoples, 1991). Data have been collected by ODWC since 1991. Biologists from ODWC established each 32-km route along secondary roads in what they determined to be typical quail habitat (Peoples, 1991) resulting in 78 routes across the entire state. Routes remained the same each year of the survey. ODWC biologists conducted bobwhite counts by driving each route either at sunrise or 1 h before sunset, and counting the number of bobwhites observed along the route. Surveys were conducted twice each year, once in August and once in October. We used the total number of bobwhites observed per route as an index of abundance. This index is positively correlated with fall hunter-harvest ($r > 0.70$, S. DeMaso, unpublished data). We averaged the August and October count for each year and standardized counts among counties by calculating the standard normal deviate for each averaged count. The standard normal deviate is calculated by subtracting the mean count for each route from each individual yearly average, and dividing this value by the standard deviation for that route. Therefore, this normalization expresses bobwhite counts as deviations from the route mean per unit standard deviation. Positive values indicate a count that was greater than the mean for a particular year corrected for variation in the data. Negative values indicate the opposite.

2.3. Climate and weather variables

Although they are often used interchangeably in the literature, we differentiate between weather, which we define as short-term rainfall and temperature patterns within years, and climate, which we define as the long-term pattern in precipitation and temperature across years. We used data from the National Climate Data Center (NCDC) from weather stations closest to each route (EarthInfo, Inc., Boulder, Colorado, USA 1997). We used mean monthly maximum temperature for June, July, and August. We selected these months because they occur during the peak of hatching and brood-rearing (Klimstra and Roseberry, 1975; Roseberry and Klimstra, 1984). We chose the maximum daily temperature rather than the minimum because these months are typically the hottest in this region of the country and, therefore, bobwhites are more likely to respond to maximum temperatures. Previous research has indicated that bobwhites avoid operative temperatures $> 39°C$ (Forrester et al., 1998), where operative temperature is a composite of air temperature, radiant energy input from the sun, and wind (Campbell and Norman, 1998, pp. 198–200). Case and Robel (1974) reported that exposure to temperatures $\geq 40°C$ was lethal for bobwhites. We used total monthly precipitation averaged for winter (December, January, and February), spring (March, April, and May), and summer (June, July, and August). We selected these months because they correspond to biologically important phases of the bobwhite's life cycle (winter survival, breeding, and recruitment).

Data were obtained for each year of the bobwhite survey (1991–1997). We constructed two databases for analyses. The first contained the actual weather values for a particular year for each of the above-described categories. This was the weather-effects database. The second database was the climate-effects database, and contained the deviation of yearly weather values from the long-term mean. We calculated these deviations by subtracting the long-term means (i.e. the mean for the entire record history [range: 30–100 years]) from the yearly data. For each year in each database, we included the standard normal deviate of the previous year's count. We included this variable to account for density-dependent effects on bobwhite production (Errington, 1945; Roseberry and Klimstra, 1984). Inclusion of this variable reduced our sample size because we had no counts prior to 1991 from which to calculate previous-year's counts.

2.4. Land-use variables

In addition to the weather and climate data, each database also included land-use variables that may also contribute to bobwhite abundance. Modeling for the variation in quail abundance contributed by land-use variables permitted greater sensitivity in analyses of weather and climate effects. We used the proportion of each county's area that was in crop production. These data were obtained from the Oklahoma Department of Agriculture's annual crop statistics reports (Oklahoma Agricultural Statistics Service, 1991–1997). These reports list county-level hectarages for a variety of crops, but do not report hectarages below ∼202 ha. Therefore, our analysis may slightly underestimate the true proportion of each county in cultivation. Another major land use in Oklahoma is livestock grazing. We used the total head of cattle per km^2 of non-cultivated land as an estimate of grazing intensity. Livestock data also were obtained from the Oklahoma Department of Agriculture (Oklahoma Agricultural Statistics Service, 1991–1997).

2.5. Neural networks

We used a multilayered, backpropagation neural network architecture (Hagan et al., 1996; Smith, 1996). Models were constructed and trained using QNet for Windows (v97.02, Vesta Services, Winnetka, Illinois, USA). Our networks had three layers: an input layer containing the independent variables, a neuron layer, and an output layer containing the dependent variable. Our network was fully connected (Smith, 1996, p. 21). The number of neurons in the neuron layer was experimentally determined by allowing the number of neurons to vary between two and nine in a series of networks, where all other parameters were held constant. We selected the model with the highest correlation between predicted counts and the validation data set (see below). Including too few or too many neurons may result in low accuracy of the network's predictions (Smith, 1996, pp. 120–123). The neurons applied a sigmoid transfer-function (Smith, 1996, p. 40; Hagan et al., 1996, pp. 2-3–2-6) to the inputs using an adaptive learning rule (Haykin, 1999).

Before network training commenced, we divided the data into two subsets. The first subset was used to train the model. Model training is the process by which the network learns the response patterns of the dependent variable or variables to variation in the independent variables (Smith, 1996, p. 50). During training, the network learns by adjusting the values of the connection weights to minimize the mean square error during the next forward pass through the network. The second subset was used to validate the model, and was not used in network training. Although not a true validation of the model (Conroy, 1993; Conroy et al., 1995; Rykiel, 1996), we believe that this technique provided a means of assessing accuracy and reliability of the network's predictions. To subdivide the data, we rank-ordered cases by normalized counts, then selecting every 5th case. Therefore, roughly 20% of our total database was used to evaluate model accuracy. There were 280 cases in the training data subset and 68 in the validation data subset.

Neural networks were trained for 5000 iterations. Preliminary analyses indicated that the change in network error had reached a plateau by this time. We used a learning rate of 0.05 and a momentum of 0.90. These values provided the best relative performance during preliminary runs. The learning rate controls the magnitude of the changes made to the connection weights, and therefore, controls the speed at which the network learns (Smith, 1996, p. 77; Hagan et al., 1996, p. 9–5). The momentum controls how many past iterations to consider when making connection-weight adjustments, and therefore, prevents the network from repeating past mistakes (Smith, 1996, pp. 85–88). The momentum also affects the speed at which the network can learn.

Trained models were used in simulation analyses to determine the nature of the relationship between predictor and response variables (Lek et al., 1996). We constructed data sets in which the variable of interest was allowed to vary between its minimum and maximum value. All other variables were held constant at their mean value. We arbitrarily decided on using the mean value because it represents, by definition, the average condition for that variable. However, it should be noted that the response we obtained using the mean value of non-target variables in the simulations may differ quantitatively from those we could have obtained using the median, for example. We did not expect major qualitative differences between the responses, however. In addition to these simulations, we also calculated the percent contribution of each individual variable to each network's predictions (Özesmi and Özesmi, 1999). This is calculated by summing the squared connection weights of each independent variable and dividing this by the sum of squared weights for all independent variables, and is a measure of the influence of each variable in the model.

To determine the relative effects of weather and climate on bobwhite abundance, we used an adjusted sum-of-squares technique (Hilborn and Mangel, 1997). This adjusts the sum-of-squares by penalizing the addition of parameters (Hilborn and Mangel, 1997). Networks with the lowest adjusted sum-of-squares account for the most variation in the data among a group of selected models, in the simplest manner. Our logic was akin to that of 'Occam's Razor': we selected the model that accounted for the most variation in annual normalized bobwhite counts corrected for the level of parameterization. The adjusted sum-of-squares criterion ($\mathrm{SS_A}$) is calculated as:

$$\mathrm{SS}_A = \frac{\mathrm{SS_m}}{n - 2m},$$

where $\mathrm{SS_m}$ is the sum-of-squared deviations for the model of interest, n is the sample size used to develop the model, and m is the number of parameters in the model (Hilborn and Mangel, 1997). We used the sum-of-squares from the training data only for making these calculations. We considered all connection and bias weights as parameters in this analysis.

3. Results

3.1. Neural models

A network with eight neurons was the best predictor of normalized bobwhite counts from weather data. This network accounted for 25% of the variation in the training data ($r = 0.50$). Maximum daily temperature in June, July, and August contributed 37% to the weather network's predictions (Table 1). The single greatest contributor to the weather network's predictions was cattle density on non-cultivated land (18%, Table 1).

A four-neuron network performed best for the climate data, accounting for 23% of the variation ($r = 0.48$). Deviations from mean July and August daily maximum temperatures collectively contributed 31.5% to the climate network's predictions, and July was the single largest contributor at 18.3% (Table 1). Deviations from mean total winter, spring, and summer precipitation contributed 42.8% to the network's predictions (Table 1).

The adjusted sum-of-squares analysis indicated that the climate network predicted the normalized bobwhite counts better than the weather model when parameterization was taken into account. The sum-of-squares for the weather model was 291.0 and for the climate model was 286.5. Each model had a sample size of 279 training cases. There were 80 parameters in the weather network and 40 parameters in the climate model. These values resulted in adjusted sum-of-squares for the weather network of 2.43 and for the climate network of 1.44.

3.2. Simulation analyses

Although all variables contributed to network predictions, some variables had relatively minor contributions. For our weather network, spring precipitation and last year's normalized counts both contributed $<10\%$ (Table 1). We therefore restrict our discussion to the remaining variables for the weather simulations. However, we provide the simulation results for the low-contribution variables in Fig. 1.

As June temperature increased past $\sim 31°C$, the weather network predicted that bobwhite counts will be less than the route mean (Fig. 1a). Below this temperature, counts were predicted to be slightly more than the route mean (Fig. 1a). An opposite trend was observed for July temperature (Fig. 1b). At July temperatures below 33°C, counts were predicted to be less than average, but above this temperature bobwhite counts increased above the mean count (Fig. 1b). August temperature had a more predictable effect, similar to that of June temperature. Bobwhite counts increased above the mean with increasing August temperature, but were less than the mean below $\sim 26°C$ and above $\sim 33°C$ (Fig. 1c).

Table 1
Independent variable contributions to neural network predictions of normalized bobwhite counts (1991–1997) in Oklahoma based on weather and climate data

Variable[a]	Percent contribution[b]	
	Weather network	Climate network
June temperature/deviation	12.0	5.0
July temperature/deviation	14.5	18.5
August temperature/deviation	11.5	13.5
Winter precipitation/deviation	11.0	17.0
Spring precipitation/deviation	2.0	13.0
Summer precipitation/deviation	13.0	12.5
Proportion of county area in cultivation	11.0	7.0
Cattle density on non-cultivated land	18.0	5.5
Previous year's normalized bobwhite count	6.0	7.0

[a] Variables for the weather network were the observed weather values for each year. Variables for the climate network were the deviations of the yearly weather values from the long-term mean weather values.

[b] Percent contribution reflects the importance of a particular variable in determining a neural network's predictions relative to other variables. Percent contribution is calculated by dividing the sum of the squared connection weights for a particular independent variable by the sum of the squared connection weights of all independent variables combined.

The weather network's predictions for winter precipitation indicated that counts continued to increase above the mean as precipitation increased above 50 mm (Fig. 1d). The effects of summer precipitation showed counts above the mean, except when precipitation was between ~ 110 and ~ 170 mm (Fig. 1f).

Land-use variables contributed substantially to the network's predictions (Table 1). The weather network predicted that bobwhite counts that were greater than the mean count when the proportion of area in cultivation exceeded 0.15 (Fig. 1g), and this relationship was nearly linear. The negative relationship between cattle density on non-cultivated lands and normalized quail counts was also nearly linear, but counts were predicted to be lower than the mean for almost all cattle densities (Fig. 1h).

Like the weather network, some variables in the climate model contributed relatively little to the network's predictions (Table 1). For the climate model, all land-use variables, last year's normalized counts, and June temperature contributed $<10\%$. Again, we restricted our discussion to variables contributing $>10\%$, but provide simulation results for all variables in Fig. 2.

Positive deviations of July temperature from the long-term mean resulted in higher bobwhite counts (Fig. 2b). Predicted counts did not fall below the mean counts until temperature deviated more than $-4°C$ from normal (Fig. 2b). However, August temperatures below the mean resulted in increased predicted bobwhite counts and temperatures above the mean by more than 2°C resulted in below average counts (Fig. 2c).

Positive deviations from long-term winter precipitation resulted in predicted counts above the

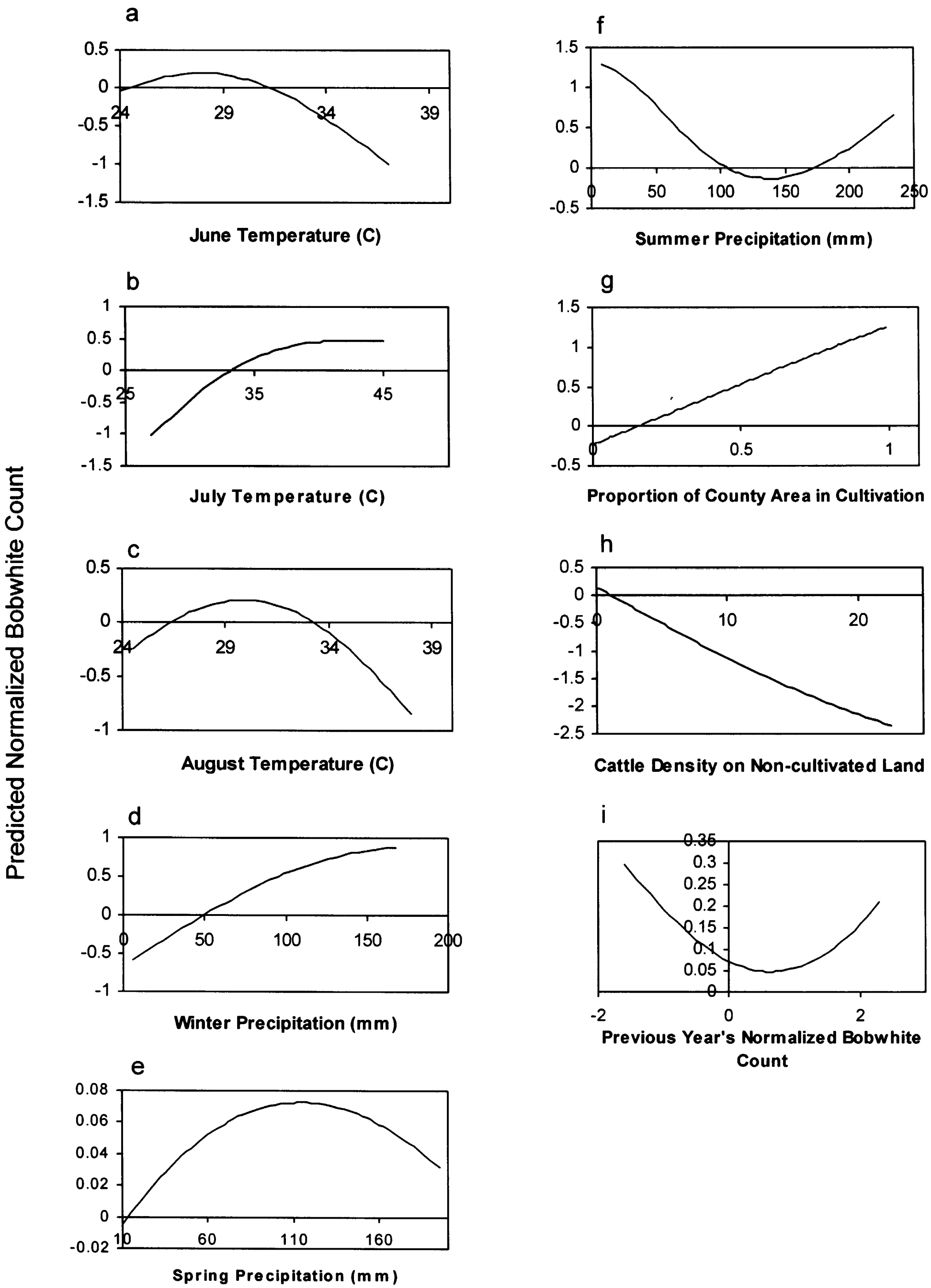

Fig. 1. Results of simulation analyses of the independent variables' effects on normalized bobwhite counts in Oklahoma using the weather neural network. Variables of interest are the observed weather conditions and landscape variables for a particular year: June (a), July (b), and August (c) temperature; winter (d), spring (e), and summer (f) precipitation; and the proportion of county area in cultivation (g), density of cattle on non-cultivated land (h), and the previous year's normalized bobwhite count (i).

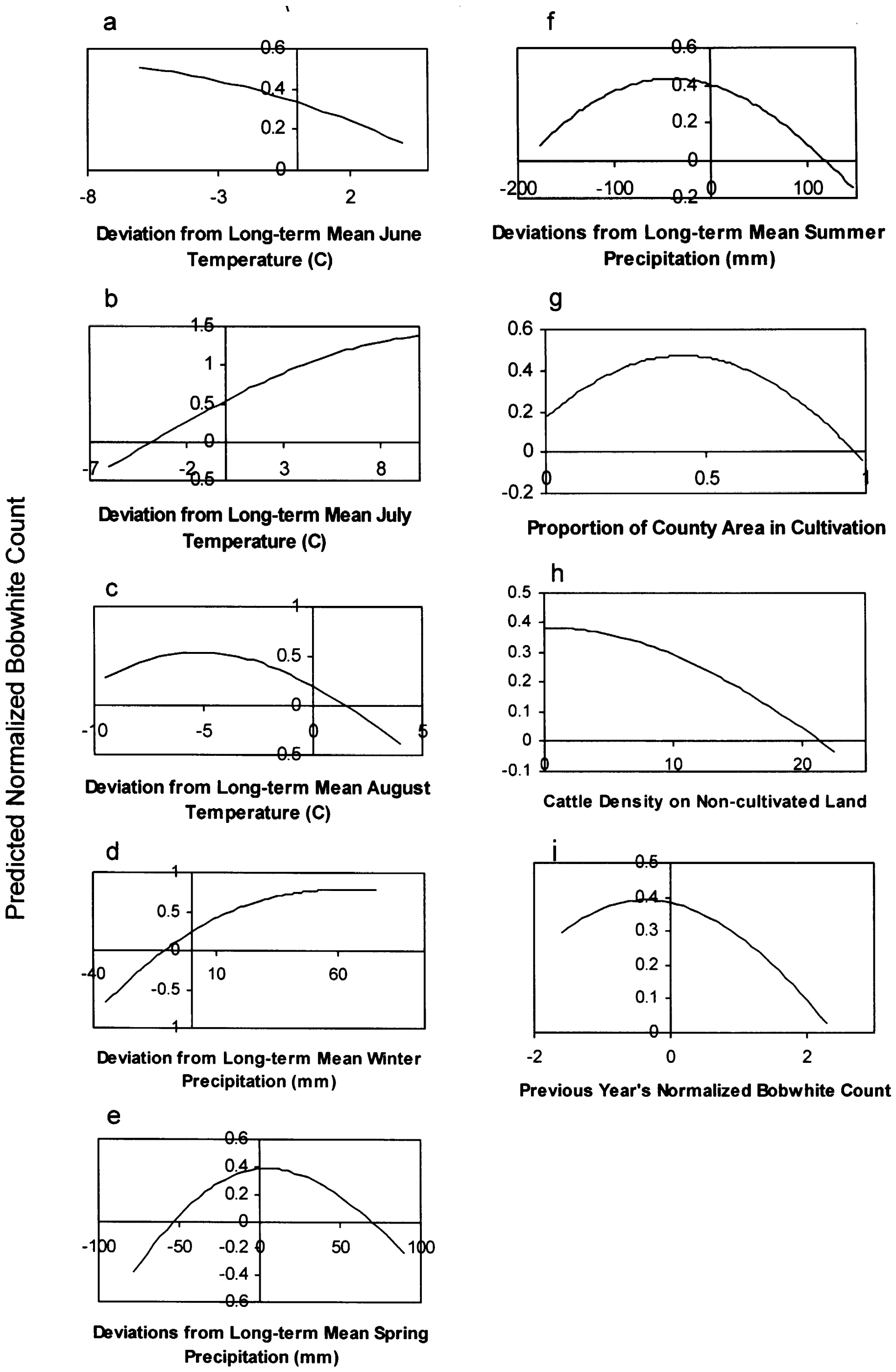

Fig. 2. Results of simulation analyses of the independent variables' effects on normalized bobwhite counts in Oklahoma using the climate neural network. The variables in this network were the deviations of annual weather conditions from long-term mean conditions and landscape variables: deviation from long-term mean June (a), July (b) and August (c) temperature; deviation from long-term mean winter (d), spring (e), and summer (f) precipitation; and the proportion of county area in cultivation (g), density of cattle on non-cultivated land (h), and the previous year's normalized bobwhite count (i).

mean (Fig. 2d). Counts did not fall below the mean until precipitation fell 30 mm below normal (Fig. 2d). Above-average counts were predicted over a wide range of deviations from mean spring rain, but were highest near the mean (Fig. 2e). Both excessive (> 70 mm above mean) and insufficient (< 55 mm below mean) spring rain resulted in below average counts. A similar pattern was observed for summer rain (Fig. 2f). However, the peak increase in predicted counts occurred when rain was ~ 40 mm below the summer mean. Bobwhite counts less than the mean were predicted only when precipitation was 130 mm or more above the summer mean.

4. Discussion

Climate changes predicted by the current generation of simulation models, if accurate, will undoubtedly have consequences for wildlife species in almost every ecosystem. Understanding the ways in which particular species are susceptible to climate change is an important first step in preparing for future management decisions. Our results showed that the climate network was more parsimonious than the weather network. Therefore, bobwhite population abundance may be more sensitive to the variation in weather from long-term mean climate conditions than to the magnitude of the weather variables. In other words, it may not be so much how much rain falls, as it is how much more or less rain falls than normal. The magnitude of the deviation from normal conditions may limit quail production or survival if bobwhites have a small thermal-tolerance around mean conditions to which they have adapted. Although the thermal neutral zone of a particular species is relatively invariant across their ranges, a species may still adapt to local, mean conditions within the thermal neutral zone. This is not to say that weather conditions do not impact populations; direct losses to weather conditions undoubtedly occur (Errington, 1936, 1939, 1941; Roseberry, 1962, 1964).

Our simulation analyses also provided insights into the relationships between climate and weather patterns and bobwhite abundance, and provided a method for assessing the accuracy of the network's predictions. Although weather effects were of secondary importance in our analyses, they can still impact survival and production. Further, most research has only investigated weather-pattern effects. So, we include the simulations from the weather network here. For June temperatures higher than ~ 31°C and August temperatures higher than ~ 33.5°C, bobwhite abundance was predicted to be below the mean abundance over the entire survey period. There was also a decrease in bobwhite abundance observed when August temperatures exceeded 1.5°C above the long-term mean. These results are in general agreement with previous research. Bobwhite production in northwestern Florida, USA, was negatively associated with summer temperature (Murray, 1958). The length of the nesting season, during a long-term study of bobwhites in southern Illinois, USA, was negatively associated with July–August temperature (Klimstra and Roseberry, 1975). This same study reported an increase in nest abandonment with increasing July–August temperature (Klimstra and Roseberry, 1975). Bobwhites avoided habitat space–time (Guthery, 1997) in which operative temperatures exceeded 39°C in Texas, USA (Forrester et al., 1998; Guthery et al., 2000), 32°C in Sonora, Mexico, and 29°C in Arizona, USA (Guthery et al., 2000). Other quail species have been reported to have similar responses to summer heat. Chick survival decreased with increasing summer heat among California quail (*Callipepla californica*) in California, USA (Sumner, 1935) and Gambel's quail (*Callipepla gambelii*) production declined with increasing July temperature in Arizona, USA (Heffelfinger et al., 1999). Simulations for July temperature showed an increase in bobwhite counts above the mean as July temperature increased or increased above the mean. Klimstra and Roseberry (1975) reported that 75% of bobwhite hatchings occur during the 9 week period between 17 June and 18 August in southern Illinois, USA. Because of the surge in juveniles during this period, temperature effects may be muted to some extent. However, high temperatures during the breeding season have been linked to reduced laying periods for bobwhites (Klimstra and Roseberry, 1975), and female bobwhites stop laying at high temperatures (Guthery et al., 1988). Furthermore, excessive temperatures, although detrimental to chicks, may be more detrimental to incubating eggs (Wilson et al., 1979). Our climate and weather networks, therefore, gave a biologically reasonable representation of summer heat effects on quail abundance. Further, our networks also indicated a possible threshold temperature below which there is little effect on production or survival. This thermal threshold may indicate the upper limit of the bobwhite's thermal-tolerance in this area of their range. We suspect that some of the above-reported results from other studies may indicate the effects of climate rather than weather. However, because these authors did not evaluate climate effects, this remains conjecture.

There was a positive effect of winter precipitation on bobwhite counts. Winter rains in excess of 50 mm and all positive deviations of winter rain resulted in higher than average bobwhite counts. Winter precipitation may enhance bobwhite production indirectly through increased spring vegetation, seed abundance, and insect densities (Swank and Gallizioli, 1954; Sowls, 1960). Other quail research supports our results. In Illinois, USA, bobwhite harvest in the fall was strongly, positively related to January and March precipitation (Edwards, 1972). Research on scaled quail (*Callipepla squamata*) in Texas, USA, indicated that abundances increased with increasing winter precipitation (Giuliano and Lutz, 1993). Summer precipitation exceeding 100 mm generally reduced predicted bobwhite counts in our network simulations. Predicted counts were higher than the mean when spring and summer rains were around the long-term mean amount. This may indicate that, for these climate variables, bobwhites have adapted to the local conditions. Brown (1978) suggested that bobwhites had evolved under a 'continental' type climate where winter rainfall is less variable and deviations from summer rain determine breeding success. Our analyses agreed somewhat with Brown's (1978) predictions. There was less variation in winter rain than in spring or summer rain. Furthermore, normalized bobwhite counts tended to be highest near mean spring and summer rain, indicating that bobwhites abundance was most sensitive to the variation in spring and summer rain. Deviations too far from the local means resulted in decreased bobwhite abundance. Sumner (1935) reported increased juvenile mortality when rains increased during the hatching season. Excessive rain in the spring and summer may increase chick mortality, especially among gallinaceous birds, whose young are poor thermoregulators the first few days after hatching (Newton, 1998). Further, because rain may limit transmission of sound waves or inhibit calling behavior, increased spring rain may depress breeding effort. However, the breeding success of Attwater's prairie chickens (*Tympanuchus cupido attwateri*) was not affected by precipitation during May, or between March and June (nesting season) (Peterson and Silvy, 1994). Again, our results were generally supported by previous research, but give an added understanding of the non-linearity in bobwhite population responses.

Land-use variables (proportion of cultivated land and cattle density on non-cultivated land) were only important contributors to the weather network's predictions, not the climate network's. Because the same land-use variables were used in both the climate and the weather models, this was somewhat surprising. However, it may indicate that there was more information about the response of bobwhite populations among the climate variables than was available among the weather variables. This supports our contention that deviations from long-term normal conditions may be more relevant to species management.

The weather network predicted bobwhite counts greater than the mean over the entire range of the proportion of cultivated land. This linear increase does not agree with other research. Bobwhite abundance in Illinois, USA, was greatest at intermediate levels of cultivation (Roseberry and Sudkamp, 1998). Within this intermediate zone, usable habitat space–time may be maximized and increased edge may favor bobwhites. At higher levels of cultivation, usable space–time decreases and edge becomes redundant (Guthery and Bingham, 1992). We are unable to clearly explain why our network predicted ever-increasing counts with increasing cultivation. Increasing cultivation should lead to a decrease in habitat space–time (Guthery, 1997). One possible explanation may be the method of route selection. Routes were established in areas containing typical bobwhite habitat (Peoples, 1991); therefore, cultivation effects may have been decoupled from bobwhite abundance. The effects of cattle density, and therefore, grazing intensity, were more straightforward. As cattle density increased, our network predicted that bobwhite counts would be lower than the mean. This agrees with other research. Grazing negatively influenced scaled quail habitat in Oklahoma, USA (Schemnitz, 1961). Interactive effects between site productivity and grazing indicated that on highly productive sites, bobwhite abundance is favored by the early successional stages maintained by more intensive grazing (Spears et al., 1993). However, on less productive sites, bobwhite abundance is higher at higher successional stages (Spears et al., 1993). Because productivity forms an east-west gradient from high to low productivity, and because grazing intensity forms an east-west gradient from low to high (pers. obs.), our simulations fit this pattern.

5. Conclusions

Our analyses indicated that bobwhite abundance might be more sensitive to the deviation of climate from the normal conditions to which they have become adapted under climate-change scenarios. Although the weather conditions within a given year can also be important, most species have probably adapted to some variation around mean conditions. Furthermore, the effects of deviations in some variables may be more important than others (Brown, 1978). It is when these deviations exceed the bobwhite's ability to cope, that survival and productivity are affected. The pace at which climate change occurs also may affect how bobwhites respond to predicted climates.

Acknowledgements

This research was supported by the Oklahoma Department of Wildlife Conservation, the Department of Forestry at Oklahoma State University (OSU), the Oklahoma Agricultural Experiment Station, the Game Bird Research Fund, the Bollenbach Endowment, and the Noble Foundation. In addition, J. Lusk was supported by a Presidential Fellowship for Water, Energy, and the Environment from the OSU Environmental Institute, and by a Eugene and Doris Miller Distinguished Graduate Fellowship from the OSU Foundation. This research was approved for publication by the Oklahoma Agricultural Experiment Station.

References

Brown, D.E., 1978. Grazing, grassland cover and gamebirds. Trans. N. Am. Wildl. Nat. Res. Conf. 43, 477–485.

Brown, J.L., Li, S.-H., Bhagabati, N., 1999. Long-term trend toward earlier breeding in an American bird: a response to global warming? Proc. Nat. Acad. Sci. USA 96, 5565–5569.

Bystrak, D., 1981. The North American breeding bird survey. Stud. Avian Bio. 6, 34–41.

Case, R.M., Robel, R.J., 1974. Bioenergetics of the bobwhite. J. Wildl. Manag. 38, 638–652.

Campbell, G.S., Norman, J.M., 1998. An Introduction to Environmental Biophysics. Springer-Verlag, New York, NY, USA, p. 286.

Church, K.E., Sauer, J.R., Droege, S., 1993. Population trends of quails in North America. In: Church, K.E., Dailey, T.V. (Eds.), Quail III: National Quail Symposium, Pratt, Kansas, USA, pp. 44–54.

Conroy, M.J., 1993. The use of models in natural resource management: prediction, not prescription. Trans. N. Am. Wildl. Nat. Res. Conf. 58, 509–519.

Conroy, M.J., Cohen, Y., James, F.C., Matsinos, Y.G., Maurer, B.A., 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecol. Appl. 5, 17–19.

Dawson, W.R., 1992. Physiological responses of animals to higher temperatures. In: Peters, R.L., Lovejoy, T.E. (Eds.), Global Warming and Biological Diversity. Yale University Press, New Haven, CT, USA, pp. 158–170.

Dunham, A.E., 1993. Population responses to environmental change: operative environments, physiologically structured models, and population dynamics. In: Kareiva, P.M., Kingsolver, J.G., Huey, R.B. (Eds.), Biotic Interactions and Global Change. Sinauer Associates, Inc., Sunderland, MA, USA, pp. 95–119.

Easterling, D.R., Horton, B., Jones, P.D., Peterson, T.C., Karl, T.R., Parker, D.E., Salinger, M.J., Razuvayev, V., Plummer, N., Jamason, P., Folland, C., 1997. Maximum and minimum temperature trends for the globe. Science (USA) 277, 364–367.

Edminster, F.C., 1954. American Game Birds of Field and Forest. Charles Scribner's Sons, New York, NY, USA, p. 490.

Edwards, W.R., 1972. Quail, land use, and weather in Illinois 1956–70. In: Morrison, J.A., Lewis, J.C. (Eds.), Proc. First Natl. Bobwhite Quail Symp., Stillwater, OK, USA, pp. 174–183.

Errington, P.L., 1936. The winter of 1934–35 and Iowa bob-whites. Am. Mid. Nat. 17, 554–568.

Errington, P.L., 1939. The comparative ability of the bob-white and the ring-necked pheasant to withstand cold and hunger. Wilson Bull. 51, 22–37.

Errington, P.L., 1941. An eight-winter study of central Iowa bob-whites. Wilson Bull. 53, 85–102.

Errington, P.L., 1945. Some contributions of a fifteen-year local study of northern bobwhite to a knowledge of population phenomenon. Ecol. Mono. 15, 1–34.

Forrester, N.D., Guthery, F.S., Kopp, S.D., Cohen, W.E., 1998. Operative temperature reduces habitat space for northern bobwhites. J. Wildl. Manag. 62, 1506–1511.

Gill, F.B., 1995. Ornithology. W.H. Freeman and Company, New York, NY, USA, p. 763.

Giuliano, W.M., Lutz, R.S., 1993. Quail and rain: what's the relationship? In: Church, K.E., Dailey, T.V. (Eds), Quail III: Nat. Quail Symp., Pratt, Kansas, USA, pp. 64–68.

Guthery, F.S., 1997. A philosophy of habitat management for northern bobwhites. J. Wildl. Manag. 61, 291–301.

Guthery, F.S., 1999. Slack in the configuration of habitat patches for northern bobwhites. J. Wildl. Manag. 63, 245–250.

Guthery, F.S., Bingham, R.L., 1992. On Leopold's principle of edge. Wildl. Soc. Bull. 20, 340–344.

Guthery, F.S., King, N.M., Nolte, K.R., Kuvlesky, W.P. Jr., DeStephano, S., Gall, S.A., Silvy, N.J., 2000. Comparative habitat ecology of Texas and masked bobwhites. J. Wildl. Manag. 64, 407–420.

Guthery, F.S., Koerth, N.E., Smith, D.S., 1988. Reproduction of northern bobwhites in semiarid environments. J. Wildl. Manag. 52, 144–149.

Hagan, M.T., Demuth, H.B., Beale, M., 1996. Neural Network Design. PWS Publishing Company, Boston, MA, USA, p. 300.

Haykin, S., 1999. Neural Networks: A Comprehensive Foundation, Second. Prentice Hall, Upper Saddle River, NJ, USA, p. 842.

Heffelfinger, J.R., Guthery, F.S., Olding, R.J., Cochran, C.L. Jr., McMullen, C.M., 1999. Influence of precipitation timing and summer temperatures on reproduction of Gambel's quail. J. Wildl. Manag. 63, 154–161.

Hilborn, R., Mangel, M., 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, NJ, USA, p. 315.

Houghton, J.T., Jenkins, G.J., Ephraurms, J.J., 1990. Climate change: the OPCC scientific assessment report prepared for IPCC Working Group 2. Cambridge University Press, Cambridge, England, United Kingdom.

Kaufman, K., 1996. Lives of North American Birds. Houghton Mifflin, Boston, MA, USA, p. 675.

Klimstra, W.D., Roseberry, J.L., 1975. Nesting ecology of the bobwhite in southern Illinois. Wildl. Mono. 41, 37.

LaRoe, E.T., 1991. The effects of global climate change on fish and wildlife resources. Trans. N. Am. Wildl. Nat. Res. Conf. 56, 171–176.

Lek, S., Belaud, A., Baran, P., Dimopoulos, I., Delacoste, M., 1996. Role of some environmental variables in trout abundance models using neural networks. Aqu. Living Res. 9, 23–29.

Murray, R.W., 1958. The effects of food plantings, climatic conditions, and land use practices upon the quail population on an experimental area in northwest Florida. Proc. Ann. Conf. Southeast. Assoc. Game Fish Commiss., 12, pp. 269–274.

Newton, I., 1998. Population Limitation in Birds. Academic Press, San Diego, CA, USA, p. 597.

Özesmi, S.L., Özesmi, U., 1999. An artificial neural network approach to spatial habitat modelling with interspecific interaction. Ecol. Model. 116, 15–31.

Peoples, A. 1991. Upland game investigations: quail monitoring, performance report. Oklahoma Department of Wildlife Conservation, Federal Aid in Wildlife Restoration project W-82-R-30.

Peters, R.L., 1992. Introduction. In: Peters, R.L., Lovejoy, T.E. (Eds.), Global Warming and Biological Diversity. Yale University Press, New Haven, CT, USA, pp. 3–14.

Peterson, M.J., Silvy, N.J., 1994. Spring precipitation and fluctuations in Attwater's prairie-chicken numbers: hypotheses revisited. J. Wildl. Manag. 58, 222–229.

Roseberry, J.L., 1962. Avian mortality in southern Illinois resulting from severe weather conditions. Ecology 43, 739–740.

Roseberry, J.L., 1964. Some responses of bobwhites to snow cover in southern Illinois. J. Wildl. Manag. 28, 244–249.

Roseberry, J.L., Klimstra, W.D., 1984. Population Ecology of the Bobwhite. Southern Illinois University Press, Carbondale, IL, USA, p. 259.

Roseberry, J.L., Sudkamp, S.D., 1998. Assessing the suitability of landscapes for northern bobwhites. J. Wildl. Manag. 62, 895–902.

Rubenstein, D.I., 1992. The greenhouse effect and changes in animal behavior: effects on social structure and life-history strategies. In: Peters, R.L., Lovejoy, T.E. (Eds.), Global Warming and Biological Diversity. Yale University Press, New Haven, CT, USA, pp. 180–192.

Rykiel, E.J. Jr., 1996. Testing ecological models: the meaning of validation. Ecol. Model. 90, 229–244.

Sauer, J.R., Hines, J.E., Gough, G., Thomas, I., Peterjohn, B.G., 1997. The North American Breeding Bird Survey results and analysis. Version 96.4. Patuxent Wildlife Research Center, Laurel, MD, USA.

Schemnitz, S.D., 1961. Ecology of the scaled quail in the Oklahoma panhandle. Wildl. Mono. 8, 1–47.

Schneider, S.H., 1993. Scenarios of global warming. In: Kareiva, P.M., Kingsolver, J.G., Huey, R.B. (Eds.), Biotic

Interactions and Global Change. Sinauer Associates, Inc., Sunderland, MA, USA, pp. 9–23.

Smith, M., 1996. Neural Networks for Statistical Modeling. International Thomson Computer Press, London, England, United Kingdom, p. 235.

Sowls, L.K., 1960. Results of a banding study of Gambel's quail in southern Arizona. J. Wildl. Manag. 24, 185–190.

Spears, G.S., Guthery, F.S., Rice, S.M., DeMaso, S.J., Zaiglin, B., 1993. Optimum seral stage for northern bobwhites as influenced by site productivity. J. Wildl. Manag. 57, 805–811.

Sumner Jr., E.L., 1935. A life history study of the California quail with recommendations for conservation and management. Calif. Fish Game 21, 167–256, 277–342.

Swank, W.G., Gallizioli, S., 1954. The influence of hunting and of rainfall upon Gambel's quail populations. Trans. N. Am. Wildl. Nat. Res. Conf. 19, 283–297.

Tracy, C.R., 1992. Ecological responses of animals to climate. In: Peters, R.L., Lovejoy, T.E. (Eds.), Global Warming and Biological Diversity. Yale University Press, New Haven, CT, USA, pp. 171–179.

Wilson, H.R., Nesbeth, W.G., Miller, E.R., Ande, T.B., Ingram, D.R., 1979. Hatchability of bobwhite quail eggs incubated in various temperature combinations. Poult. Sci. 58, 1351–1354.