NORTHERN BOBWHITE ABUNDANCE IN RELATION TO CLIMATE, WEATHER, AND LAND USE IN ARID AND SEMIARID AREAS: A NEURAL NETWORK APPROACH

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PREFACE

Some of the chapters in this dissertation have been published in peer-reviewed journals. Although I shared authorship of these chapters in their published form with colleagues and collaborators, I am responsible for the content (analysis, modeling, and writing). Because each chapter was meant to be a stand-alone manuscript, some duplication of information is necessary. Therefore, I have elected to leave each chapter in its published form. Footnotes at the beginning of each chapter indicate the manuscript's status and, if applicable, the full citation for published chapters. Authors wishing to cite information in the published chapters should cite the published versions, since these journals own the copyrights. I attempted to limit the amount of repetition in chapters that have not been previously published. As a result, the introductions and discussions in these chapters, particularly Chapter 6, are shorter than their counterparts in published chapters.

I would like to thank my advisor, Dr. Fred S. Guthery, for his guidance and encouragement during my studies at Oklahoma State University (OSU). He has been both a mentor and a colleague, and it has been an honor to have worked with him. He encouraged me to challenge existing knowledge and pervading paradigms, and provided a role model to emulate. I thank Dr. Samuel D. Fuhlendorf for serving on my committee, for his constructive and detailed comments on numerous manuscripts, and for his perspectives on landscape ecology and rangelands. I would also like to thank my other committee members, Drs. Ronald Masters and Stanley Fox for their assistance and advice. Several people have made my time in Stillwater more enjoyable. Most notably, I would like to thank Kim Suedkamp Wells, Heather Hansen (née Wilson), Charles Coley, Jill Brison, and Jon Forsman for their friendship, support, and encouragement. C. Coley also provided moral support and editing assistance during the writing of this dissertation. Finally, I would like to thank my parents for their constant love and support, even though they still are not certain what it is that I do.

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CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW[1]

The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) is an important game species over much 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 in numbers between and among years (Stoddard 1931, Stanford 1972, Roseberry and Klimstra 1984:130). Possible factors influencing long-term trends in bobwhite abundance include climate change, habitat loss, and land-use changes (Edwards 1972, Klimstra 1982, Brady et al. 1993, Schemnitz 1993, Rotenberry 1998). Further, harvest may be an additive, rather than compensatory, 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 stable, huntable populations, an understanding of the factors influencing bobwhite abundance that are not amenable to management, such as weather and climate, is required. It is further required that the interactions between climate, weather, and land use be elucidated, because it is against the backdrop of these effects that habitat and harvest management must operate.

Another issue of some importance is the effects of global change on wildlife, especially in the arid and semiarid regions of the United States (Guthery et al. 2000). As such, global change is an issue of concern to both conservation and wildlife management. With the knowledge garnered from investigations of the responses of bobwhite abundance to current climate, weather, and land-use patterns, managers may be better able to plan for the effects of

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[1] This chapter was written to place the remaining chapters into a common context. It is not intended for publication.

future climate, as predicted by various global-change models. Such planning will be a necessary part of any long-term management program (Irwin 1998), and could involve reserve-site choice or habitat manipulations designed to ameliorate the effects of climate.

In the United States, bobwhites range over much of the eastern and central parts of the country (Kaufman 1996). According to data from the North American Breeding Bird Survey (NABBS), bobwhite populations in the US show a long-term rate of decline of 2.40% per year (Church et al. 1993, Sauer et al. 1997). This rate of decline increased between 1982 and 1991 to 3.50% 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). However, short-term trends indicate a significant decline. The 10-year population trend for the period 1986-1996 indicates a 3.88% per year decline, and the 3-year trend (1993-1996) indicates populations are declining at a rate of 7.26% per year (Sauer et al. 1997). In Texas, the long-term rate of decline is 2.00% per year, with short-term declines of 6.43% per year (10-year trend) and 20.09% per year (3-year trend) (Sauer et al. 1997).

Although the above-cited declines may be cause for concern among wildlife managers, these changes in average abundance through time provide a reference frame from which to determine population status. As mentioned previously, bobwhite populations tend toward boom-or-bust dynamics across their range (Stoddard 1931, Stanford 1972, Roseberry and Klimstra 1984:130). In the US, the mean number of bobwhites counted per NABBS route over the years 1966–1996 was 20.95. In Oklahoma and Texas, the mean was 47.12 and 33.21, respectively (Sauer et al. 1997). Considering shorter intervals, the 10-year mean in Oklahoma is 44.59 bobwhites per NABBS route, and in Texas 26.37 bobwhites per NABBS route. The 3-year means for 1993–1995 are 37.83 and 21.55 bobwhites per NABBS route in Oklahoma and Texas, respectively (Sauer et al. 1997). Therefore, trends in bobwhite populations may not be as severe as suggested by the percent declines.

The importance of various weather factors in determining avian abundance varies both with the species being considered and with latitude. Temperature is a controlling factor in northern latitudes, especially over the winter period. In southern latitudes, rainfall and moisture tend to be more important than temperature (Newton 1998:288), but summer temperature can also have important effects on the reproductive biology of a species (Leopold 1933, Robinson and Baker 1955, Speake and Haugen 1960, Guthery et al. 2001), thereby influencing abundance measured in the autumn. Among gallinaceous birds, young are often susceptible to both rainfall and temperature (Sumner 1935, Newton 1998:288).

Weather effects may manifest both through direct and indirect means. Direct effects such as hyper- and hypothermia are obvious, but weather's indirect effects may be more difficult to detect. Weather may act indirectly on abundance through both food availability and habitat suitability (Swank and Gallizioli 1954, Sowls 1960, Newton 1998), and may be moderated or accentuated by both the length and intensity of the weather event (Leopold 1931, Elkins 1995). For example, insect prey is essential for successful brood-rearing among quail (Hurst 1972), and the availability of such prey is determined, in part, by rain and temperature (Elkins 1995). Periods of drought and high temperature will reduce the amount of insect prey available and, therefore, reduce production (Newton 1998:289). Further, these impacts on production might increase in magnitude with the length of the drought. In addition, the effects of weather on a species are not constant, but vary with the average physical condition of the local population. If a drought is of sufficient duration, the population may be food stressed and less able to withstand the vagaries of weather than a population that has not experienced a food shortage, but exposed to the same weather conditions (Newton 1998:289).

Rainfall and temperature both influence quail dynamics (Edwards 1972, Stanford 1972, Campbell et al. 1973, Roseberry and Klimtstra 1984, Giuliano and Lutz 1993), but the effects vary with region. Investigations of weather effects also differ in how they define weather variables, such as summer rain, and in the estimates of population parameters used. Consequently, reported results are not directly comparable and often lead to confusion about the exact effects of weather on quail production and population status.

In arid regions, rainfall is the most influential weather component for avian survival and production (Newton 1998), is an important determinant of abundance, and can affect various demographic components of bobwhites. In drier environments in south Texas, the bobwhite's breeding season ends 2 months earlier than in more mesic environments (Guthery et al. 1988). Summer rainfall (April–August) was highly, positively correlated with hunter success for scaled quail (*Callipepla squamata*) in eastern New Mexico (Campbell 1968). Rainfall may be more critical during certain periods of the life cycles of quail species than during other periods. Heffelfinger et al. (1999) found that mid-winter (December–January) rainfall affected calling behavior of Gambel's quail (*Callipepla gambelii*) more than rainfall during early (October–November) or late (February–March) winter. In arid and semiarid regions of Oklahoma and Texas, spring and summer rainfall might be particularly important (Stanford 1972). However, Campbell et al. (1973) did not find a significant correlation between May–June or April–July rainfall and scaled quail production in New Mexico. A lack of linear correlation between environmental and response variables may not necessarily indicate a lack of relationship between the variables (Laasko et al. 2001). Summer rainfall (July–August) had the greatest influence on scaled quail production (Campbell et al. 1973), with most of the response due to August rainfall alone (Campbell 1968). Percent juveniles in the fall bobwhite harvest was positively related to the average total rainfall between May and August in Alabama (Speake and Haugen 1960). Bobwhite production in Louisiana responded positively to increasing summer precipitation, with highest production occurring when precipitation exceeded 762 mm (Reid and Goodrum 1960). June rainfall in Texas was only weakly related to bobwhite abundance (Giuliano and Lutz 1993).

Recent work by Bridges et al. (2001) in Texas showed that, although 12-month rainfall totals were positively correlated with bobwhite abundance in the South Texas Plains, the 12-month Modified Palmer Drought Severity Index (PMDI; an index of rainfall that accounts for soil type and moisture, temperature, and evaporation) was more strongly correlated with bobwhite abundance. They also reported that monthly PMDIs were positively correlated with bobwhite abundance in the Cross Timbers and Prairies (November–February, $r_s \geq 0.57$), Edwards Plateau (September–November, $r_s \geq 0.59$), Rolling Plains (September–February, April, June; $r_s \geq 0.56$), and South Texas Plains (October–July, $r_s \geq 0.56$), whereas raw rainfall amount was positively correlated with bobwhite abundance only in the South Texas Plains.

Although snowfall sufficient to kill bobwhites occurs in parts of their range, snowfall is probably not a major concern in arid and semiarid regions. In these regions, however, winter rainfall can still influence quail production. The effects of winter rain, again, vary by species and region. Percent juveniles in fall populations of scaled quail showed a non-significant, negative relationship with winter (October–March) rainfall both in pre- and post-harvest samples (Campbell et al. 1973). However, in an earlier study of scaled quail in the same area, winter rainfall (October–March) showed non-significant, positive correlation with hunter success, which is assumed to be an index of abundance (Campbell 1968). Giuliano and Lutz (1993) found that scaled quail abundance in Texas was positively correlated to winter rainfall. Bobwhite harvest in Illinois was positively related to winter rainfall (Edwards 1972), whereas, in Texas, abundance showed a non-significant, negative correlation with winter rainfall (Giuliano and Lutz 1993). California quail (*Callipepla californica*) age ratios were positively correlated with winter (January–March) rainfall in California (Francis 1970).

Temperature may be a less important factor in quail production than rainfall (Edwards 1972), or may only be important below some critical threshold of precipitation (Robinson and Baker 1955, Heffelfinger et al. 1999). However, this might not hold for arid and semiarid regions where operative temperatures may exceed the thermotolerance limits of many species (Forrester et al. 1998, Heffelfinger et al. 1999, Guthery et al. 2001). In such areas, high temperatures reduce the amount of space–time available for use by a species (Guthery 1997, Forrester et al. 1998, Heffelfinger et al. 1999). Klimstra and Roseberry (1975) reported that July–August (summer) temperatures affected the end of the bobwhite nesting-season. Therefore, the effects of temperature will be of critical importance to bobwhite production in the more southern areas of its range, if temperatures increase due to global change.

Forrester et al. (1998) found that bobwhites avoided patches in which the operative temperature (a metric that takes account of the ambient air temperature plus the heating effects of sunlight and the cooling effects of airflow) exceeded 39 °C and, as a result, 50% of the available habitat space–time was unusable to bobwhites during all seasons. The age ratio of bobwhite populations in Louisiana in winter responded positively to mean maximum monthly temperature in all months, but responded negatively with the highest maximum monthly temperature (Reid and Goodrum 1960). Therefore, high seasonal temperatures can affect production. For example, the length of the laying season in Illinois was reduced by 12 days for every 1 °C increase in the July–August temperature (Klimstra and Roseberry 1975). In Alabama, the percent juveniles in the fall harvest was negatively correlated with the total deviation from mean monthly temperatures from May through August (Speake and Haugen 1960). Reid and Goodrum (1960) reported that bobwhite production was suppressed in hot years compared with cooler years. Hot, dry conditions reduced the percentage of female bobwhites in laying condition in south Texas (Guthery et al. 1988). Male bobwhites reduced calling behavior by 86.4% in a hot year compared with a cooler year (Guthery et al. 2001). It seems likely that bobwhites adjust their reproductive activities based on ambient weather conditions in a particular year, thereby favoring long-term survival and maximizing lifetime reproductive output. However, other studies in higher latitude areas lacked a strong effect of temperature on production and recruitment. For example, Edwards (1972) did not find consistent effects of mean monthly temperature on bobwhite harvest in Illinois. Further, Roseberry and Klimstra (1984) found no relationship between bobwhite recruitment and mean average daily temperature or mean maximum daily temperature. Although temperature reduced the length of the bobwhite breeding-season, it did not decrease the proportion of those young produced in a given year from entering the breeding population. That is, juvenile survival was not reduced.

The effects of temperature and rainfall can interact in influencing bobwhite abundance. Rainfall masked the effects of temperature on bobwhite production in Kansas (Robinson and Baker 1955). When precipitation was below some threshold amount, temperatures above 23.3 °C reduced bobwhite production, but there was little effect when rainfall exceeded this threshold (Robinson and Baker 1955). Combinations of low rainfall (drought) and high temperatures reduced bobwhite recruitment (Stanford 1972, Hurst et al. 1996). Guthery et al. (2002) report that temperature and rainfall influence age ratios of bobwhites in south Texas in complex, non-linear ways, and suggest that low temperatures can mitigate the negative effects of drought and that high temperatures can eliminate the positive effects of rainfall.

Habitat provides all life requisites for an individual organism (Hall et al. 1997), and is, therefore, an important factor in understanding a species abundance and distribution. Human use of the landscape can have considerable effects on its suitability as habitat for wildlife. Whereas the amount of land area converted for human use influences population dynamics, the spatial pattern of this fragmentation is also of concern (Hanski 1999). Further, different land uses will affect wildlife populations to different extents. That is, not all land-use practices are incompatible with wildlife. Human land use practices fall into 2 broad categories: 1) urban development resulting in land being converted to residential, commercial, or industrial use, and 2) agricultural development resulting in land being converted to the production of food for humans or domesticated animals. Although cropland is a dominant agricultural land use in the northern and eastern portions of the bobwhite's range, in the west, grazing may be more pervasive. Around 70% of western land area is grazed (Fleischner 1994). In Texas, approximately 53,140,000 ha, or 76.8% of the land area, is in agriculture, with 65.5% of that area rangeland and 28.7% cropland (USDA NASS, Census of Agriculture 1997). In Oklahoma, approximately 13,443,000 ha, or 74.2% of the land area, is agricultural land, of which 46.5% is rangeland and 44.7% is cropland (USDA NASS, Census of Agriculture 1997). Therefore, grazing and cultivation are important land uses that affect the amount of usable habitat space–time (Guthery 1997) available for bobwhites. As the predominant land use in these states, livestock grazing and cultivation undoubtedly influence the abundance, distribution, and population dynamics of a variety of wildlife species (Barnes et al. 1991).

The conversion of habitat from native vegetation to row crops often converts what was once a heterogeneous landscape into a monoculture. Early agricultural practices, typified by many, small family-owned farms, resulted in a pattern of land use referred to as patchwork agriculture and was believed to enhance wildlife abundance through the creation of edge between cultivated fields and windbreaks and fencerows (Leopold 1933). Modern agricultural practices, however, are managed using “clean farming” practices, which favor large fields with few fencerows or windbreaks.

Cultivated crops may serve as a food source for some wildlife species. Roseberry and Klimstra (1984) report that unharvested grain served as the only food source for bobwhite coveys during a prolonged snow cover in southern Illinois. The benefit to bobwhites from these unharvested grains depends on the juxtaposition of standing crops to suitable bobwhite winter habitat. In southern Illinois, much of the agricultural landscape is still in a patchwork arrangement (J. Lusk, personal observation) and, therefore, such juxtapositions occur frequently. However, the value of food plots and cultivated cropland for bobwhites in other areas where such juxtapositions are rare is probably nil, mostly because bobwhite populations cannot survive in such landscapes.

Livestock grazing does not usually result in the total transformation of the vegetation community, but, depending on the intensity and periodicity, can alter the structural complexity and species composition of the habitat and thereby affect its suitability (Fleischner 1994). Whether these habitat changes will increase or decrease suitability depends on the magnitude of the changes (Severson and Urness 1994). Further, changes that favor a particular species may disfavor another species (Barnes et al. 1991, Severson and Urness 1994). Structural changes include changes in vegetation stratification leading to a reduction in structural complexity (Fleischner 1994). Grazing can also reduce the amount of litter and increase the amount of bare ground, which in some cases can alter plant phenology (Kaufman et al. 1983). Changes in litter and ground cover can increase soil compaction and thereby reduce water infiltration (Orr 1960, Orodho et al. 1990), which can have nontrivial effects on plant communities, especially in arid and semiarid regions (Fleischner 1994). Grazing was the primary influence on grassland species composition in the Edwards Plateau ecoregion in Texas (Fuhlendorf and Smeins 1997, Fuhlendorf et al. in press). However, interannual precipitation was correlated with plant basal area (Fuhlendorf et al. 2001). Precipitation and grazing also interacted in determining species composition, where moderately and ungrazed areas were more resilient to the effects of severe drought than heavily grazed areas (Fuhlendorf and Smeins 1997). These grazing effects on the vegetation community will indirectly affect bobwhite abundance.

Bobwhites have adapted to a variety of habitats from the eastern coast of the United States west to the Rocky Mountains. Within these longitudes, bobwhites have adapted to conditions from temperate latitudes in Wisconsin to subtropical, semiarid, and arid latitudes throughout the southern US and south to Costa Rica. Within the array of habitats the bobwhite occupies, there are many configurations of habitat types that are equally optimal (Guthery 1999). Many authors have qualitatively described bobwhite habitat in various regions. For example, Edminster (1954) reported bobwhite habitat included grassland, cropland, brushy cover, and woodland habitat types. In south Texas, optimal habitat configuration typically consisted of 53% woody canopy coverage, 38% herbaceous canopy coverage, and 44% bare ground (Kopp et al. 1998). In southern Illinois, bobwhites were associated with patchy landscapes with moderate levels of grassland and row crops, and high levels of woody edge (Roseberry and Sudkamp 1998).

Although there is a great deal of ecological slack in the optimal composition of bobwhite habitat (Guthery 1999), the structural changes brought about by grazing could have the greatest impact on bobwhite abundance. Grazing may increase the amount of bare ground in an area (Fleischner 1994) and decrease amounts of certain grass species

(Severson and Urness 1994). These changes have been associated with increases in bobwhite use (Schulz and Guthery 1988). Peak bobwhite abundance occurred in pastures using a rapid-rotation grazing system compared to abundances under continuous grazing (Hamerquist and Crawford 1981, Schulz and Guthery 1988). Given that the optimal seral stage for bobwhites varies with the overall productivity of the habitat (Spears et al. 1993), the effects of grazing on bobwhite abundance may also vary among areas and habitat types.

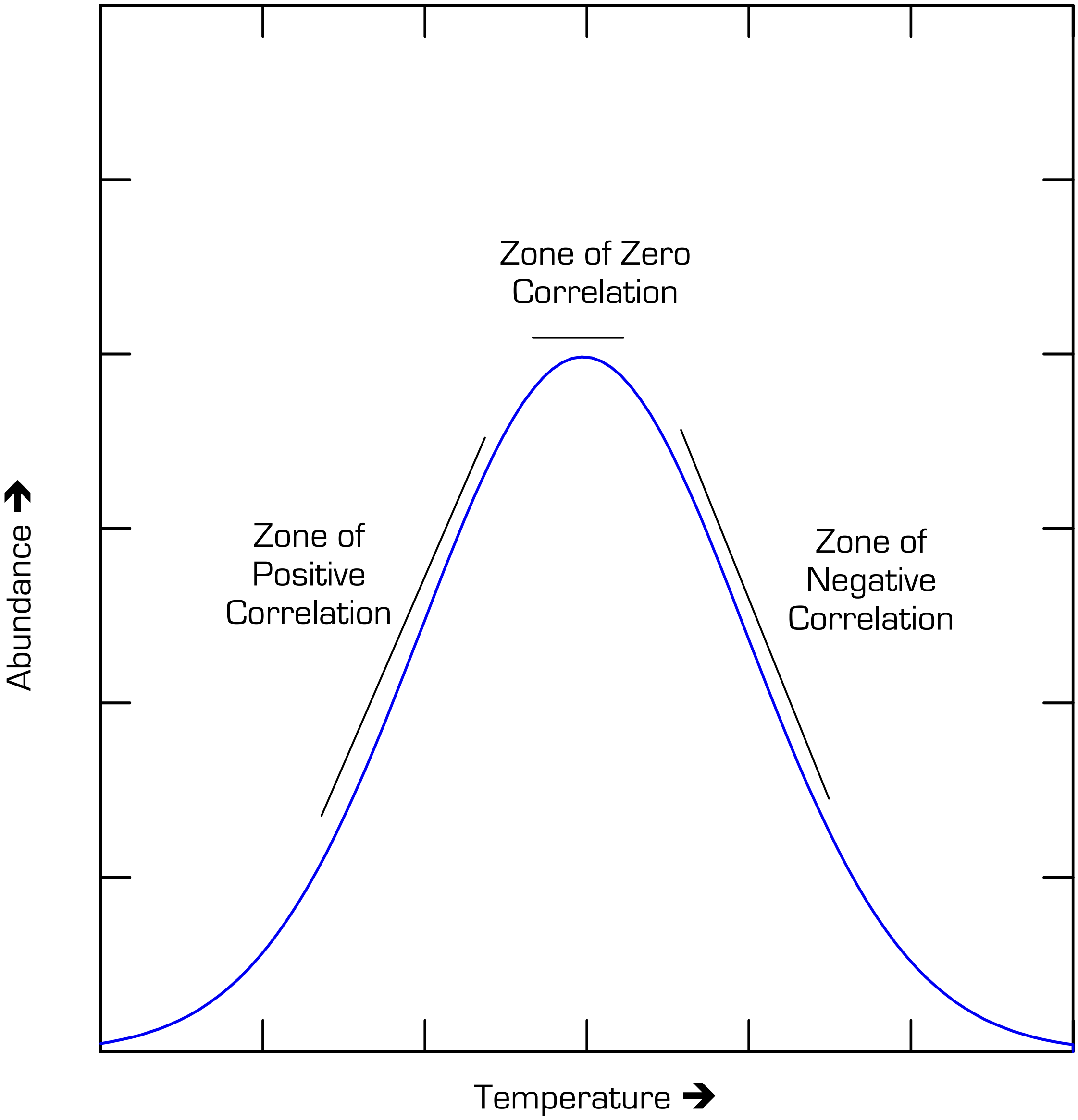
The research reported herein was intended to address several issues of importance to bobwhite management in the arid and semiarid regions of their range, and attempted to address some of the current ambiguity apparent in previous investigations of bobwhite–weather relationships. I employed an artificial neural network technique to model bobwhite abundance in relation to climate, weather, and land use. I then used these models to predict the changes in bobwhite abundance that could be expected under equilibrium climate expected under 2x the current CO_2 concentrations in the atmosphere (IPCC 1998).

The research reported herein is important for several reasons. First, little research into the population dynamics of grassland birds has been undertaken to date, despite the fact that declines among these species have been of greater magnitude and of a more persistent trend than for the more-studied, neotropical-migrant forest species (Herkert and Knopf 1998, Rotenberry 1998). Conservation efforts for many grassland species-of-concern are hampered by a lack of data on aspects of their ecology (Herkert and Knopf 1998). Further, because indirect methods are commonly used to obtain demographic data, estimates of demographic parameters based on these data might be biased or imprecise (Pollock et al. 1989, Shupe et al. 1990, Clobert and Lebreton 1991, Roseberry and Klimstra 1992). The nature of the relationship between bobwhite production and climate, weather, and land use is unclear at this time. This lack of clarity results from a multitude of studies with largely contradictory results. These contradictions might result from differences in variable definition and selection, or from the use of linear analysis techniques. Linear analyses, such as correlation and regression, are not conducive for determining functional relationships among variables when the functional relationship is nonlinear. For example, correlation coefficients may indicate a positive or negative response to variation in another variable, but the lack of a strong correlation may not be indicative of a lack of relationship between the variables (Laasko et al. 2001). Furthermore, nonlinear biological responses to environmental variation can sometimes result in either spurious positive or negative correlations depending on the functional response of the biological system and the pattern of environmental variation (Laasko et al. 2001). For instance, 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 correlation coefficients, even when temperature is a strong forcing variable for bobwhite abundance (Fig. 1.1). Therefore, a nonlinear analysis approach is necessary to clarify these relationships and to confirm or reject results obtained using traditional linear approaches.

Second, the neural models resulting from my analyses were used to predict bobwhite abundance in the fall, prior to the hunting season. As such, the Oklahoma Department of Wildlife Conservation and the Texas Parks and Wildlife Department can use them to forecast fall harvests in advance of their fall roadside counts, thereby giving them more time to act on this information. This information may also be used by managers and conservation biologists to develop proactive management plans in the light of global climate change. Because the bobwhite is an important game species, its management and conservation are of immediate concern to state wildlife managers. Declining bobwhite populations could lead to decreased revenue from the sale of hunting licenses and decreased funding from contributions to the Federal Aid in Wildlife Restoration program, and, therefore, these state agencies must begin planning to minimize the impact climate change might have on bobwhite populations within their jurisdictions.

Third, research is only a part of the management process. To be useful for management, research must be conveyed to managers in a manner in which they can apply it to the decision-making process (Hejl and Granillo 1998, Young and Varland 1998). My

Fig. 1.1. Hypothetical relationship between abundance and temperature showing how the range over which a variable is measured in the field can determine the response type. Even if sampling crosses the depicted zones, the overall correlation might still be negative, positive, or nonexistent.


Zone of Zero Correlation
Zone of Positive Correlation
Zone of Negative Correlation
Abundance ➔
Temperature ➔

research will provide managers with both a method for forecasting fall bobwhite harvests and for understanding bobwhite responses to weather conditions. The former provision will assist in setting bag limits, season lengths, and in redirecting hunters from low abundance areas. In addition, the results can be used to develop long-term management plans.

Finally, the results of this research can be used to better understand the impacts of climate change on species abundance and distribution in the central United States. Evidence for the effects of climate change on species ecology continues to mount. Changes in plant phenology will have concomitant effects among vertebrate species that rely on them for food or shelter. Many species have evolved life-history characteristics synchronized with seasonal changes in resource availability, but that are only weakly coupled to actual changes in the resource (Myers and Lester 1992, Root 1993). That is, species might synchronize their life history with resource availability via proximate cues (e.g., photoperiod). Changes in climate might alter or negate the relationship between the cue and the underlying resource (e.g., plant seed abundance), resulting in a decoupling of life history from resource base, and reduction in production and abundance. Community structure will also likely be affected by climate change, because each species in the community will respond to changes differently. However, such changes in community structure will result in changes in community dynamics, which will also affect the individual species.

Although the models presented herein cannot address all of the complexities of the impacts of climate change on bobwhite populations, they can show how abundance and distribution will change in response to climate change alone. From this base, management actions can be focused on areas in which bobwhite abundance is predicted to be greatest or the least. Also, further research can begin to investigate the interactions between climate, land-use, and community reorganization.

CHAPTER 2

NEURAL NETWORK MODELING: AN APPROACH TO DISCRIMINATION AND PREDICTION[1]

Abstract

Neural network modeling offers wildlife biologists a powerful technique for finding patterns in large, multivariate datasets. Because neural network modeling is appearing more frequently in the ecological literature, we provide a descriptive overview of this approach to data analysis in wildlife research, and discuss its merits and drawbacks. Neural networks offer a powerful alternative to traditional prediction and discrimination models, especially where little or no a priori information about the relationships among variables exists. Neural networks are nonparametric, can model linear and non-linear relationships, are unaffected by multicollinearity, and can be applied to prediction and discrimination problems; the same model can simultaneously predict multiple dependent variables or discrimination classes. However, because of the structure of neural networks, biological interpretation of model output is not straightforward and requires additional simulations. Further, neural models can become overfit and lose the ability to generalize to new data. Focusing on 1 type of neural network, the backpropagation, multi-layer perceptron, we provide a prediction and a discrimination example of the technique using published data.

Introduction

An artificial neural network (ANN) is one of a suite of machine learning techniques currently being applied in ecology (Fielding 1999*b*). Other machine learning techniques include

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genetic algorithms (Mitchell 1998, Jeffers 1999) and cellular automata (Dunkerley 1999). Although other types of ANNs exist (Boddy and Morris 1999), the type we describe is a feed-forward, backpropagation multi-layer perceptron (Smith 1996; hereafter MLP). We chose the MLP because it is the simplest and most widely used technique in the ecological literature. This type of neural network was originally developed as a model of cognition and learning in the human brain (Rumelhart et al. 1986, Smith 1996, Boddy and Morris 1999, Stevens-Wood 1999). As such, the associated terminology borrows heavily from neurobiology (Table 2.1).

The use of neural network models in ecology is increasing and current applications include statistical modeling. The technique is non-parametric and, therefore, makes no distributional assumptions about the data. Applications thus far have dealt with comparing the performance of MLPs with that of traditional statistical methods. These comparisons have typically shown that MLP models out-perform more traditional analyses such as linear regression based on accuracy of predictions (Recknagel et al. 1997, Maier et al. 1998). For example, Olson and Cochran (1998) applied a MLP to model aboveground biomass in the tallgrass prairie. Compared to a regression model, their MLP model more accurately predicted standing biomass and predicted changes in biomass with greater accuracy (Olson and Cochran 1998). An MLP predicted the species diversity of arthropod assemblages in wet-soil habitats more accurately than a multiple linear regression analysis (Lek-Ang et al. 1999). Özesmi and Özesmi (1999) compared the performance of a MLP with that of logistic regression in the classification of locations in a GIS database. These locations represented either nest or non-nest sites for red-winged blackbirds (*Agelaius phoencies*) and marsh wrens (*Cistothorus palustris*). They reported that in all but 1 case the MLP outperformed logistic regression (Özesmi and Özesmi 1999). Manel et al. (1999) compared MLPs with logistic regression and multiple discriminant analysis for predicting bird-species occurrences, and

Table 2.1. Definitions of terms used in neural modeling, listed alphabetically.

Term	Definition
Backpropagation	An algorithm that sends errors detected in the output sequentially back thought the model to adjust synaptic and bias weights (parameters)
Bias weight	Weights attached to each neuron in the neuron and output layers; analogous to an intercept in a regression equation
Hidden layer(s)	One or more layers of neurons in a multi-layer perceptron; also called a neuron layer and the layer of processing elements
Input layer	Layer containing the input nodes (independent variables) in a multi-layer perceptron
Input node	Data used as predictors; synonymous with independent variables in traditional statistical models
Learning	The iterative change in synaptic weights resulting in a reduction of the mean square prediction error; the process of finding relationships among variables and producing an appropriate response for a give set of input data; also called training
Learning rate	A value determining the magnitude of changes made to the synaptic weights during the training process
Learning rule	A rule governing how a synaptic weight can be adjusted to minimize the mean square prediction

Table 2.1. Continued.

Term	Definition
Learning rule, Con't	error; examples include steepest descent and conjugate gradient
Momentum	A value determining the number of past iterations to consider when adjusting synaptic weights; reduces instabilities and oscillations in the prediction error
Multi-layer perceptron	A type of neural network model which uses a backpropagation technique to simulate cognition and learning in the brain; used in statistical modeling to find non-linear and linear patterns in large, multivariate datasets without assumptions inherent in parametric techniques
Neural network	A machine learning technique used to simulate the function of the brain
Neuron	A component of the neuron layer of a multi-layer perceptron; transforms the weighted sum of the input variables using a transfer function such as the sigmoid transfer function
Neuron layer	One or more layers of neurons in a multi-layer perceptron; also called the hidden layer and the layer of processing elements
Output layer	Layer containing the output node(s) in a multi-layer perceptron

Table 2.1. Continued.

Term	Definition
Output node	Data being predicted by a multi-layer perceptron; synonymous with the dependent variable in traditional statistical models
Overfitting	A problem in modeling in general and neural modeling in particular in which a model too closely approximates the data used for model development, and which, therefore, generalizes poorly to new data
Processing elements	One or more layers of neurons in a multi-layer perceptron; also called the hidden layer or neuron layer
Relevance	An index of the contribution of each input variable to the predictions; a measure of the importance of an input node based on the synaptic weights
Logistic transfer function	A transformation applied to the weighted sum of input variables in order to approximate the underlying function or relationships among input and output variables
Stimuli	Another way of referring to the input data in a neural network model which maintains the neurological analogy

Table 2.1. Continued.

Term	Definition
Synaptic weights	Weights applied to the input variables and neurons in order to produce accurate predictions of the output variable and which are adjusted during the learning process; contain information about the relationships among input and output data; analogous to regression coefficients
Training	See learning.
Training data	Data used during the training process to determine patterns among input and output variables and to adjust synaptic weights to minimize the mean square prediction error; a portion of the total dataset from which the MLP learns
Validation data	Data used during or after the training process to evaluate the MLP's performance to prevent overfitting and determine how well the MLP predicts from novel data; data not used to adjust synaptic weights during training

found that the MLP correctly classified more cases than the other 2 methods. However, they concluded that, based on Receiver Operating Characteristic plots (Fielding 1999*a*), the logistic model was the better model, but that it was sensitive to the prevalence of positive cases (occupied sites) in the data (Manel et al. 1999). Using an adjusted sum-of-squares technique, which penalizes models for their complexity (Hilborn and Mangel 1997), we found that a multiple linear regression model outperformed a neural model in predicting bobwhite (*Colinus virginianus*) abundance based on weather and land-use characteristics (Lusk et al. 2002). However, the neural model provided a better understanding of how bobwhite populations respond to climate.

In addition to the above comparisons between traditional statistical techniques, other researchers have applied MLP models to a variety of research questions. Multi-layer perceptron models successfully predicted call counts and age ratios for Gambel's quail (*Callipepla gambelii*) from precipitation and temperature data (Heffelfinger et al. 1999); occurrences of 3 small-bodied fish in freshwater streams in >80% of the cases (Mastrorillo et al. 1997); and abundances of trout (*Salmo trutta*) based on habitat characteristics (Baran et al. 1996, Lek et al. 1996*a*). A MLP model allowed wildlife managers in southern France to predict the impact of wild boar (*Sus scrofa*) damage to agricultural crops allowing more-efficient use of limited funds (Spitz and Lek 1999). In our research, we have applied MLP models to predict northern bobwhite abundance in western Oklahoma (Lusk et al. 2002) and to determine the relative importance of long-term climate and short-term weather patterns in determining their abundance (Lusk et al. 2001).

Multi-layer perceptrons can provide accurate predictions for management planning and decision making (Lein 1997), and a deeper insight into the ecological and biological processes at work (Colasanti 1991, Edwards and Morse 1995, Lek et al. 1996*b*). The main advantage of the MLP is that it can find patterns in large, multivariate datasets without the assumptions inherent in regression and other techniques. This is true because a MLP represents a function as a sum of terms, and any continuous function, under mild constraints, can be represented as a sum of terms. Wildlife researchers may be familiar with other sum-of-terms models, such as the kernel estimator used in home-range estimation (Worton 1989) and the Fourier series used in line transect analyses (Buckland et al. 1993).

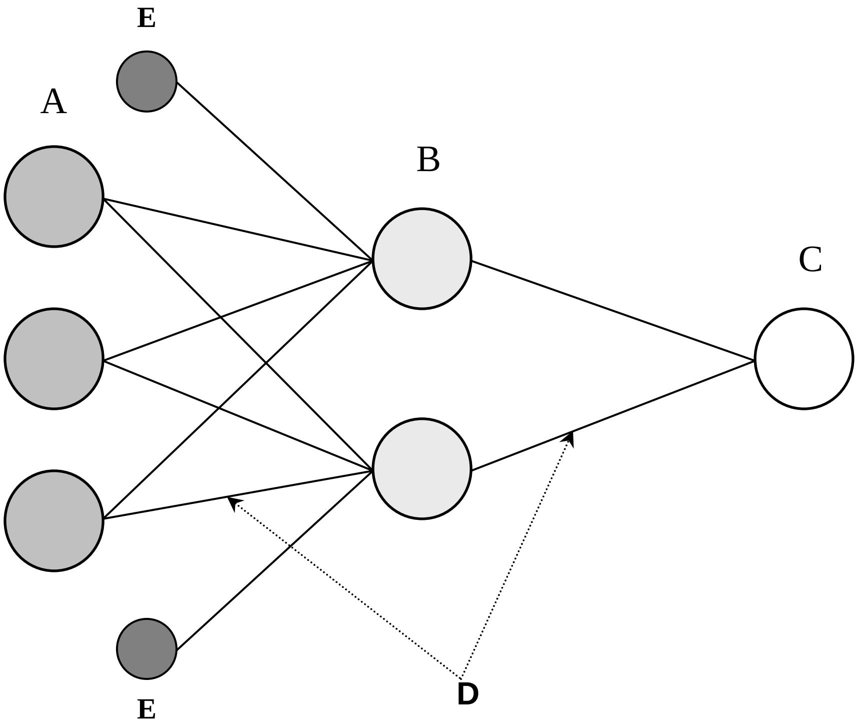
Our objective is to introduce MLP modeling to wildlife managers and scientists. We 1) briefly explain the theory behind neural modeling, 2) describe the structure and terminology of the neural modeling method, with specific regard to the MLP, 3) provide examples of the application of neural models to the problems of prediction and discrimination, and 4) discuss the strengths and weaknesses of the approach.

Model Description

Neural Model Architecture

The MLP may be arranged in a series (≥ 3) of layers (Fig. 2.1). The first layer is called the input layer, which contains 1 input node for each independent variable. Input nodes are homologous to the independent variables in multiple regression. The input nodes can be considered stimuli in the neurological sense. The second layer is referred to as the hidden layer, the neuron layer, or the layer of processing elements. The neuron layer contains ≥ 1 set of neurons, the number of which determines the complexity of patterns that can be detected (Smith 1996:25). The neuron layer processes the data to predict the dependent variable(s) in the third layer, called the output layer. The output node(s), or dependent variable(s), represent the desired response. Elements in each layer may be connected to every element in the preceding layer via synaptic weights. The synaptic weights store the information learned (see below) by the network during the training process, and are analogous to regression coefficients (Heffelfinger et al. 1999), but their interpretation is not as straightforward. Typically, each node in 1 layer is connected to every node in the preceding layer (Fig. 2.1), and, as such, the neural network is termed fully connected (Smith 1996, Boddy and Morris 1999).

Fig. 2.1. A diagrammatic representation of a generic multi-layer perceptron, neural network model. This MLP is a 3-2-1 network (3 input nodes, 2 neurons, and 1 output node) consisting of 3 layers: an input layer (A), a neuron layer (B), and an output layer (C). Nodes in 1 layer are connected to nodes in the preceding layer via synaptic weights (D). Each neuron also has an associated bias weight (E).


E
A
B
C
D
E

The Training Process

The development of a MLP model can be thought of as a process in which a network attempts to learn an appropriate response (e.g., a population abundance or a classification of used or unused) to a given set of stimuli. Training (or learning) is simply the rote method (see below) of adjusting parameters (biases and synaptic weights) such that prediction or discrimination becomes more accurate as parameters are iteratively adjusted. Biologists are familiar with least-squares regression using linear models, which attempt to maximize prediction accuracy by minimizing the sum-of-squared errors. The MLP operates under the same error minimization goal. However, because of non-linearity and other model complexities, there is no analytical solution for minimization; the model must minimize error by using a learning rule that changes synaptic weights iteratively, so that the mean squared error may be reduced each iteration. During this process, which is called training (or learning), the synaptic weights begin to represent the relationships among input and output variables. In this way, the model is said to learn.

Initially, a MLP has little or no ability to predict or discriminate because synaptic weights are set at small, random values (Smith 1996:22). Each neuron processes the incoming stimuli by first multiplying each input by the appropriate synaptic weight (Hagan et al. 1996:2-7—2-8). These products are then summed together and a bias weight is added (Hagan et al. 1996, Smith 1996). The bias weight is analogous to the intercept in regression analysis. This result, u, is then transformed using a transfer function. The most widely used transfer function is the logistic transfer function

$$\mathrm{g}(u) = \frac{1}{1+\mathrm{e}^{-u}}.$$

The use of a logistic transfer function allows non-linear relationships between the independent and dependent variables to be detected and learned. The processed stimuli, $g(u)$, are then sent to an output node. At the output node, another transformation is applied to the processed stimuli, the result of which is a scaled prediction of the dependent variable(s) (Smith

1996). This second transformation can be the same as that applied at the neurons, but more often a linear transformation is applied (Hagan et al. 1996). The model predictions can be considered a response to the incoming stimuli. Next, the predictions generated by the model are compared with the actual values of the dependent variable(s). The prediction error is calculated and backpropagated through the network to adjust the synaptic weights. Backpropagation means that the biases and synaptic weights are first adjusted for the synapses between the neurons and the output nodes, and then adjusted for the synapses between the neurons and the input nodes; i.e., information on error is sent backwards through the model. The error is apportioned among the various synaptic weights using the chain rule of calculus (Haykin 1999:162).

The adjustment of synaptic weights is governed by 3 factors. The first is the learning rule, which determines how the MLP will adjust the synaptic weights. There are several types of learning rules, the most popular of which are steepest descent and the conjugate gradient learning rules. The steepest-descent rule alters the synaptic weights after each pass through the entire dataset so that the error decreases the fastest (Smith 1996:78). A variation to the steepest-descent rule involves adjusting synaptic weights after each data point is processed, rather than after all data points have been processed. The conjugate gradient rule involves the second-order derivative (i.e., the derivative of a derivative) of the error, which measures the rate at which that slope is changing, or, in other words, the rate at which the change in error is decelerating (Smith 1996:184). The other techniques all involve the first-order derivative of the error, which gives the slope of the error surface (see below) for a given set of synaptic weights. The conjugate gradient technique, therefore, allows more accurate and sensitive adjustment of the synaptic weights, but is more computationally intense.

Related to the learning rules is the learning rate. The learning rate determines the absolute magnitude of the changes in the synaptic weights based on the direction and magnitude of the prediction error (Smith 1996:77). So whereas the learning rules determine how the synaptic weights are changed, the learning rate determines how much the synaptic weights are changed given a specific learning rule. The selection of an appropriate learning rate is important in neural model construction. If the learning rate is too small, then it will take longer for the network to learn the patterns in the data (i.e., converge to a minimal error), because only small adjustments are made to the synaptic weights. If the learning rate is too large, then the error will tend to oscillate and the network will be unstable (i.e., the predictive accuracy of the model will change from good to poor repeatedly), because the large changes to the synaptic weights will often increase the error rather than reduce it (Hagan et al. 1996:9-5, Smith 1996:81-82). We recommend using a steepest-descent learning rule with an adaptive learning rate that will allow the learning rate to be adjusted as needed during the training process (Hagan et al. 1996:12-12—12-14, Smith 1996:88-90). For example, if during training, the error begins to oscillate, the algorithm will reduce the learning rate until the oscillations are dampened and the error decreases.

The final factor governing synaptic weight changes is called momentum and determines the degree of influence past changes in the synaptic weights have over current changes (Smith 1996: 85-88). Momentum is a kind of filter, which reduces the amount of oscillations in the prediction error (Hagan et al. 1996:12-10). The momentum can have a value between 0 and 1. The larger the momentum, the stronger the effect of past error changes in determining current weight changes. Therefore, the change in the error rate after the most recent iteration will tend to continue in the direction of previous changes, even if the error begins to increase in an opposite direction. This allows weight changes to track the average error rate (Hagan et al. 1996:12-10). Because oscillations in the error rate reduce the efficiency of the training process, a high momentum, usually 0.9, is most often used (Smith 1996: 86).

Data Considerations

General Considerations. Although the specific formatting of a dataset will depend on the specific neural network application being used, there are some common data requirements. First, all data in the neural model must be numeric (i.e., consist of numbers rather than letters). Categorical and other non-numeric data, therefore, must be coded (using dummy coding, for example) for use in a neural network. Multi-layer perceptron models can predict multiple dependent variables simultaneously (Smith 1996: 165). For example, Özesmi and Özesmi (1999) used a MLP with 3 output nodes to simultaneously predict the probability that a given location was suitable as a red-winged blackbird nest site, suitable as a marsh wren nest site, and not suitable as a nest site based on habitat variables. Dependent variables can be continuous values (e.g., abundance indices) or class factors (e.g., present vs. absent; poor, fair, or good) to be predicted by the model. However, the manner in which the data are coded differs slightly from typical coding schemes. For example, presence and absence data are commonly coded as either 0 (absent) or 1 (present). This coding scheme is appropriate if these data are to be used as independent variables in a MLP model. However, if the purpose is to discriminate presence from absence based on some habitat features, the data should be recoded as some value <1 and >0, such as 0.1 (absent) and 0.9 (present). This coding scheme is necessary because the logistic transfer function approaches but does not reach 0 or 1 (Smith 1996:166), and therefore, a MLP can never predict presence or absence with complete accuracy if 1 or 0 are used for coding the dependent variable(s). A benefit of the MLP approach to discrimination is that, unlike logistic regression, MLPs can discriminate >2 classes simultaneously. For example, an MLP can discriminate poor, good, fair, and excellent habitats based on sets of habitat features.

Sample size is also an important consideration for the application of neural network models. The larger the sample size, the more information there is in the data about the relationship between the independent and dependent variable(s) for the network to learn. Therefore, it is desirable to have as large a database as possible. This is especially true if the relationships are complex or if the data are noisy (Smith 1996:115, Boddy and Morris 1999:57). For neural networks, the sample size required for a given level of accuracy is a function only of the noise in the data (Smith 1996:135).

Because neural network models become increasingly complex as the number of neurons and predictors increases (see below), the choice of variables used to predict the dependent variable should be selected with care based on extensive literature review and current knowledge about the factors affecting the system. Further, although multicollinearity is not a problem for neural models (they simply learn the redundancies in the predictors), including several correlated variables will unnecessarily increase model complexity.

Training and Validation Data. The development of a neural network model requires 2 datasets, 1 set for training the network and 1 set for validation. Training data are used during the learning phase to develop the network's synaptic and bias weights. The validation data are not used in model development (i.e., the prediction errors associated with validation data are not used to adjust synaptic weights), but are used to gauge the network's ability to respond appropriately to novel data.

Although model validation is an important part of the modeling exercise, including statistical modeling, few authors attempt to validate their models. Ideally, the data used in model validation should be independent of those used in model development (Conroy 1993, Conroy et al. 1995, Haefner 1996:157). However, in practice, data are a precious commodity and obtaining an independent dataset may be logistically or fiscally impossible. Furthermore, the intended purpose for the model must be considered when selecting a model validation approach (Rykiel 1996).

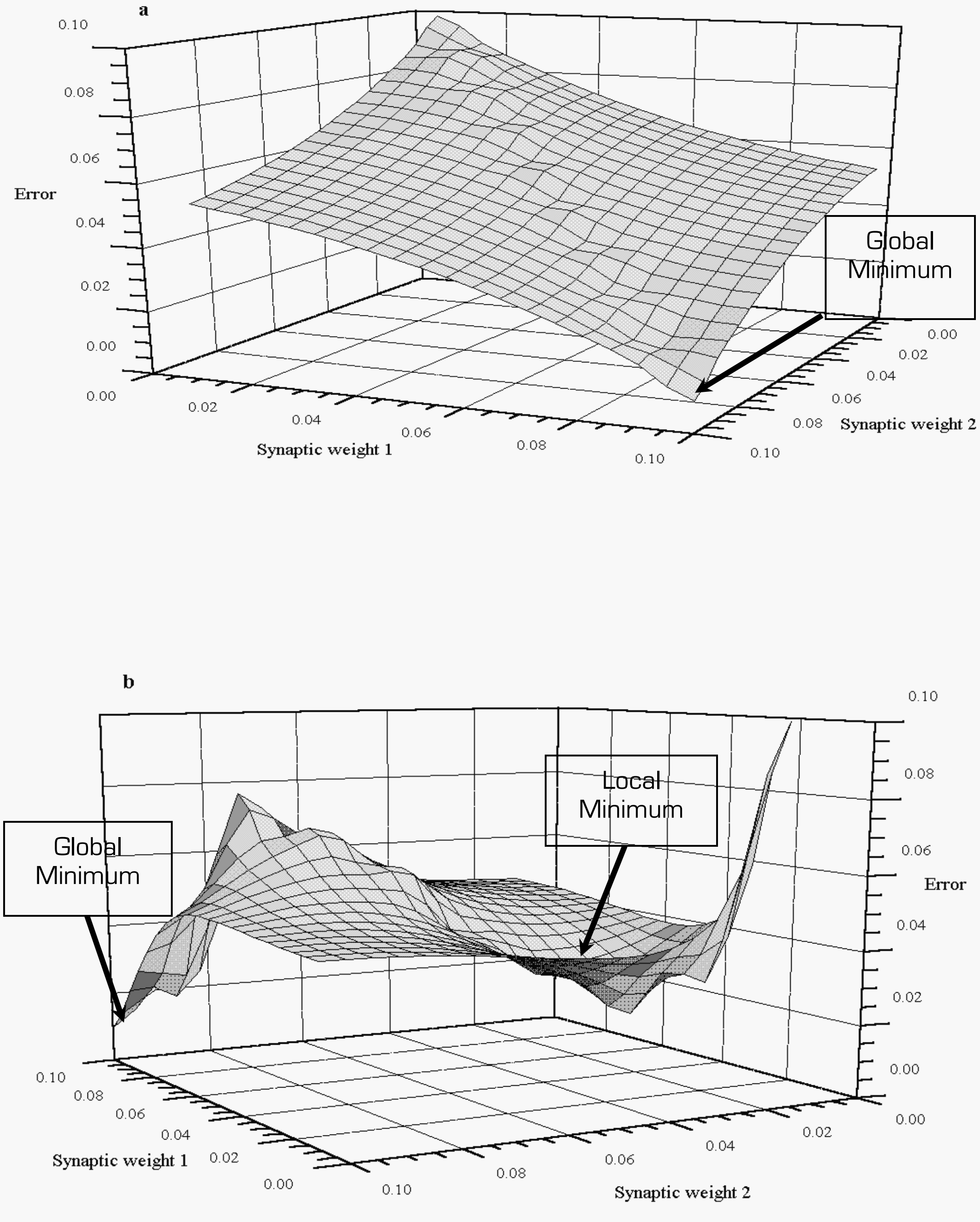
Because independent data are often lacking, data obtained during a research project must be partitioned into training and validation sets (Fielding 1999*a*:219). The first decision to be made in the partitioning of the dataset is what percentages of the total dataset should be allocated to training and validation. With more training data, a neural network has more information about the relationships among variables on which to base its predictions; therefore, as many data as possible should be allocated to the training dataset (Fielding 1999*a*:219). We generally use 80% of our data for training and 20% for validation.

After choosing the number of data points to apportion to each dataset, cases must be selected. Data may be randomly assigned to the validation dataset. However, because there are no assumptions of normality for data used for neural network training, a random sample may result in unrepresentative training and validation datasets, which has been linked to the poor generalization ability of MLPs in some applications, especially discrimination (Ripley 1994). We, therefore, recommend that the selection of training and test cases be performed using a systematic approach. For example, Lusk et al. (2002) ordered their data based on the dependent variable and systematically selected every fifth case for the validation dataset. This ensured that the training and validation data were representative of the whole dataset, and, by assumption, of the range of possible datasets.

Usage Considerations

The Error Surface. Consider a simple neural network model consisting of 2 input nodes, 1 neuron, and a single output node. The prediction error for such a model can be represented graphically as a 3-dimensional surface, where the error rate is presented as a function of the synaptic weights of each input node (Fig. 2.2). This surface represents the theoretical range of possible prediction errors for a given range of synaptic weights. Such surfaces can either be relatively flat (Fig. 2.2a) or can contain many hills and valleys (Fig. 2.2b). Because the initial synaptic weights are assigned randomly, where the network starts learning on the error surface varies. If the error surface has a relatively flat slope, the network will continue learning until the lowest point on the error surface (the global minimum) is reached. If, however, the error surface is irregular, the network will continue learning until it reaches a minimum error rate (i.e., changing synaptic weights in any direction will lead to an increase in error), but there is no guarantee that this minimum is the global minimum (Fig. 2.2b). The network may be stuck in a local minimum if other synaptic weight combinations can provide a lower prediction error. However, this problem can be ameliorated by selecting the

Fig. 2.2. Hypothetical error surfaces resulting from particular combinations of synaptic weights. In (a), the error surface is relatively flat, and a MLP with initial synaptic weights randomly assigned any value in this range will eventually find the combination of synaptic weights that gives the global minimum prediction error. In (b), the error surface is hilly. A MLP may not be able to find the combination of connection weights resulting in a global minimum, but instead may become stuck in a local minimum.


a
Error
0.10
0.08
0.06
0.04
0.02
0.00
0.00
0.02
0.04
0.06
0.08
0.10
Synaptic weight 1
0.00
0.02
0.04
0.06
0.08
0.10
Synaptic weight 2
Global Minimum
b
Global Minimum
Local Minimum
Error
0.10
0.08
0.06
0.04
0.02
0.00
0.10
0.08
0.06
0.04
0.02
0.00
Synaptic weight 1
0.10
0.08
0.06
0.04
0.02
0.00
Synaptic weight 2

appropriate number of neurons in the neuron layer (Smith 1996:62). As the number of neurons in the network increases, the error surface smoothes out and becomes more flat. Selecting the appropriate number of neurons can be accomplished by training several neural models on the same data, with the same learning rate and momentum, but with varying numbers of neurons. The network with the appropriate number of neurons will be the network with the smallest prediction error for both the training and the validation datasets and for which the addition of more neurons does not greatly increase the network's performance.

Complexity and Parsimony. Any modeling attempt must balance the costs of added complexity in terms of loss of generalization ability and the benefit of added complexity in terms of reduced variance. This is often called the bias-variance dilemma (Geman et al. 1992). The solution is based on the principle of Occam's razor (principle of parsimony) which suggests that the appropriate model is the one that is just complex enough to adequately represent the relationships in the data but no more complex (Burnham and Anderson 1998:23). However, there is no inherent reason that a simple model should be better than a more complex model, especially if the system is known to be complex (Maurer 1999), and the choice of a model will depend on the objectives of the researcher (e.g., prediction or understanding processes). That is, if a model is used solely to predict in the realm of management, then the most accurate model may be optimal, whether or not it represents the best compromise between bias and variance.

With regards to neural networks, we need to ask if the increase in complexity that accompanies neural networks provides sufficient increases in understanding or predictive power to warrant their use instead of a simple, linear model. As some authors have noted, directly comparing the predictive accuracy of both types of models is biased because the number of parameters in each model is not considered (Lek-Ang et al. 1999). Although Haykin (1999:219-222) offered several methods to limit the complexity of neural networks during training, we employ a simpler, post hoc method for ranking models. This technique adjusts the sum-of-squared errors based on the number of parameters in the model (Hilborn and Mangel 1997:114-117):

$$SS_a = \frac{SS_j}{(n-2m)},$$

where SS_a is the adjusted sum-of-squares, SS_j is the sum-of-squares for model j, n is the sample size, and m is the number of parameters in the model. The best model is the one with the smallest adjusted sum-of-squares. For a multiple linear regression, the number of parameters equals the number of regression coefficients in the model plus the intercept. Given a regression equation with 5 independent variables and 1 dependent variable, there are 6 parameters in the model. For fully connected MLPs, the number of parameters equals the number of synaptic weights and biases according to

$$m = N(I + 1) + O(N + 1),$$

where N = the number of neurons, I = the number of input nodes, and O = the number of output nodes. For example, a fully connected MLP with 5 input nodes, 3 neurons, and 1 output node would have m = 22 parameters. It is apparent that neural networks quickly grow in parameterization with the addition of predictors and neurons.

Neural Model Interpretation

Once a neural network has been trained, it can be used to generate predictions, including discrimination scores, based on new data. In addition to generating predictions, neural models can be used to increase understanding about the patterns and relationships in the data, and to generate hypotheses for further testing. There are several methods for obtaining such information from neural models. First, you can calculate the relevance (importance) of each input variable (Özesmi and Özesmi 1999):

$$R_i = \frac{\sum_{j=1} \left(w_i^2 \right)}{\sum_{n=1} \left(\sum_{j=1} \left[w_i^2 \right] \right)},$$

where, for a MLP with n input nodes and j neurons, R_i is the relevance of the ith input variable and w_i is the synaptic weight(s) associated with the ith input variable. Therefore, the relevance is the sum of squared synaptic weights for the ith input node divided by the sum of squared synaptic weights of all input nodes, and is a measure of the relative contribution of each input variable to the determination of network predictions. Variables with larger relevance values have stronger relationships with the dependent variables than those with smaller relevance values, i.e., they contain more information about the variation in the dependent variable than less relevant variables. This is true because input variables with larger synaptic weights exert more control over the network's response to a given stimulus.

The second method for obtaining biologically significant information from a neural network model is using neural interpretation diagrams (NID) (Özesmi and Özesmi 1999). These diagrams appear similar to Fig. 2.1, but the lines representing the synaptic weights are of varying widths and colors. The width of the synapses is determined by the relative values of the synaptic weights and the color of the lines by the sign (+ or –) of each synaptic weight. Therefore, the NID indicates which variables are exerting more influence over network predictions, as well as whether they are having a positive or negative influence. However, as the number of input nodes and neurons increases, the interpretation of the diagrams becomes less straightforward.

Simulation with a trained MLP model offers another alternative for interpreting the output of a neural network (Lek et al. 1996*a*). This method offers a view of how each input variable influences the value of the dependent variable. Some neural modeling software packages contain modules for automatically running a simulation analysis (e.g., Neural Connections, SPSS, Inc.). For other neural packages, a little more work is involved. First, a series of datasets must be constructed in which the independent variable of interest is allowed to vary between its minimum and maximum value, or over ±1 SD of the mean, while all other independent variables are held constant at their mean, or some other biologically meaningful value. These datasets are then presented to the trained model and a set of predictions is produced. By plotting these predicted values against the range of values for the input variable of interest, we obtain a picture of how the dependent variable responds to variation in the independent variable being considered, all else being equal. If the interactive effects of 2 variables are of interest, a dataset in which values for these variables are allowed to vary together while the remaining variables are held constant can be constructed and presented to the trained network. Predictions can then be plotted in 3-D, producing a response surface.

Accuracy Assessment

Because there are no significance tests associated with MLPs, there are no *P*-values by which to judge a model's performance and extract biologically significant information. Depending on whether you are using the neural network to predict or to discriminate, there are several options for assessing the performance of the network. The most commonly used method for predictive models is to calculate the squared correlation (r^2) between predicted and observed values.

Simulation analyses offer a way of visualizing the effect of a single variable on the dependent variable. However, simulations actually represent the effect of the variable of interest when all other variables are at their mean. It is theoretically unlikely that such average conditions will be experienced in nature, rendering the usefulness of simulations in making management decisions uncertain. The data used to train the model can be used to determine how well the simulations represent reality, however. We can filter the observed data for cases in which all observations of independent variables are within ± 1 SE of the mean. These cases can then be plotted with the simulation data to give a measure of the accuracy of the simulation predictions. With small datasets with a large number of independent variables, it might be necessary to increase the range of SE used so that there are sufficient cases available to plot.

There are several methods of determining the accuracy of discrimination models, many of which are summarized by Fielding and Bell (1997), all of which are applicable to neural network output (Fielding and Bell 1997, Fielding 1999b). The simplest method for assessing the accuracy of a classification model is to calculate the percent correctly classified. However, if misclassification errors are more important to the application, then an alternative method, called receiver operator characteristic (ROC) plots, are a better alternative, because they use all available information about the performance of the neural model (Fielding 1999b), and do not rely on a specific cut-off threshold (e.g., 0.5; Fielding and Bell 1997). The area under the ROC curve (AUC) is a measure of the performance of the network and varies between 1 and 0.5. As values approach 1, the model's performance increases. That is, if you drew a random case from both classes (i.e., 0, 1), the AUC would give the probability that the discrimination score for the case from class 1 would be greater than the score for the case from class 0 and, therefore, allow you to accurately discriminate the pair independent of a threshold cutoff. Both ROC plots and the AUC can be produced with standard, desktop statistical software (e.g., SIGNAL module in SYSTAT; SPSS Inc. 1999).

Examples

Here we provide 2 simple examples of the application of MLP modeling. The first example uses data on the relationship between Gambel's quail production and December–April precipitation (Swank and Gallizioli 1954). The second example shows how the same modeling technique can be used for discrimination, using data on habitat use by masked bobwhites (*C. v. ridgwayi*) (Guthery et al. 2001). These examples are intended to illustrate the application of the MLP technique to the analysis of ecological data as well as to show the benefits of their application.

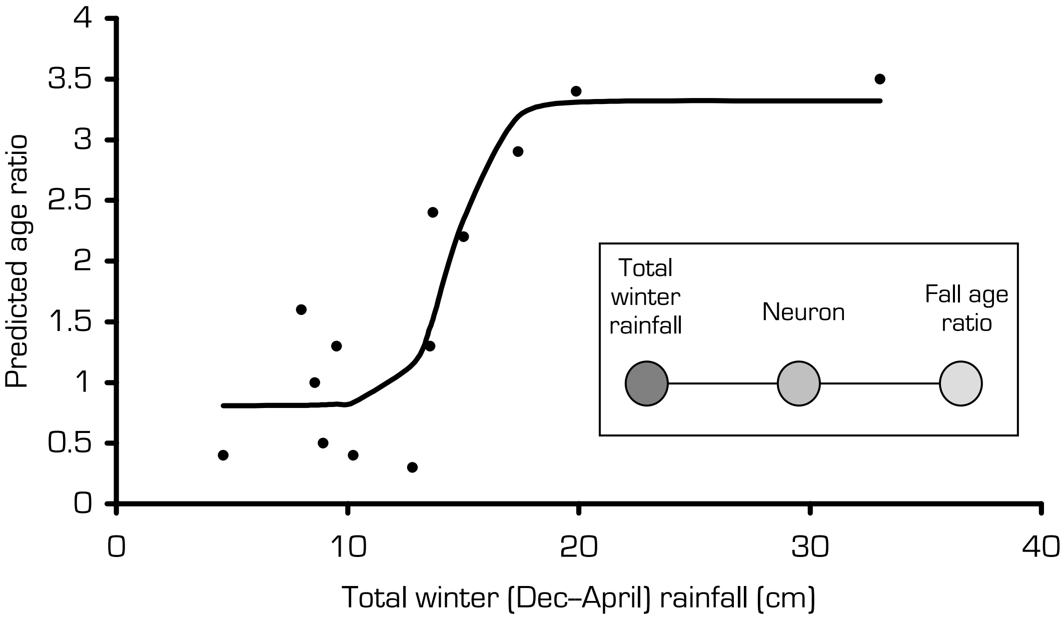
Gambel's Quail and Winter Precipitation

We used data from Swank and Gallizioli (1954) on a study conducted between 1941 and 1953 in Arizona. These data consisted of total winter (December–April) precipitation (cm) and the age ratio (juveniles/adult) in the subsequent fall harvest. Therefore, we had 1 input (total winter rainfall) and 1 output (fall age ratios) node in the network. Because we had only 1 predictor variable (rainfall), we trained a network that consisted of a single neuron (Fig. 2.3 inset). Therefore, the network consisted of 4 parameters (1 synaptic weight between the input node and the neuron, 2 bias weights for the neuron and output node, and 1 synaptic weight between the neuron and the output node). The network was trained for 400 iterations with an adaptive learning rate and a momentum of 0.6. Because of the small sample (n = 13), we did not partition the data into training and validation sets; doing so would have reduced the performance of the network (Fielding 1999*a*:219). The network accounted for 81% of the variation in the age ratios. Although the original analysis by Swank and Gallizioli (1954) did not include an estimation of trend, the authors concluded that precipitation during winter was the factor limiting abundance during their study. Our simulation analysis (Fig. 2.3) indicated that there was a relationship between fall age ratios and the previous winter's total precipitation. However, this relationship appears to be a curvilinear, logistic-like relationship (Fig. 2.3). Production (as represented by fall age ratios) was low over a wide range of total winter rainfall, but increases sharply when winter rainfall exceeds 12 cm. However, there appears to be an upper threshold of approximately 20 cm, after which there is no further increase in production with increasing precipitation. This pattern makes sense, since there is likely an upper limit to the production in any year based on time and physiological constraints (Guthery and Kuvlesky 1998). Although the relationship could have been modeled using a variety of logistic growth functions, the strength of the MLP technique is that we did not have to specify the form of the function a priori. Had the relationship been merely asymptotic rather than logistic, the MLP would have performed equally well.

Nest-site Characteristics of Northern Bobwhites

The same technique used above for prediction can, with minor modifications, be used in a discrimination analysis. We used data collected on the Mesa Vista Ranch in Roberts County, Texas, USA, during 2001 and 2002. Data were collected at northern bobwhite nest

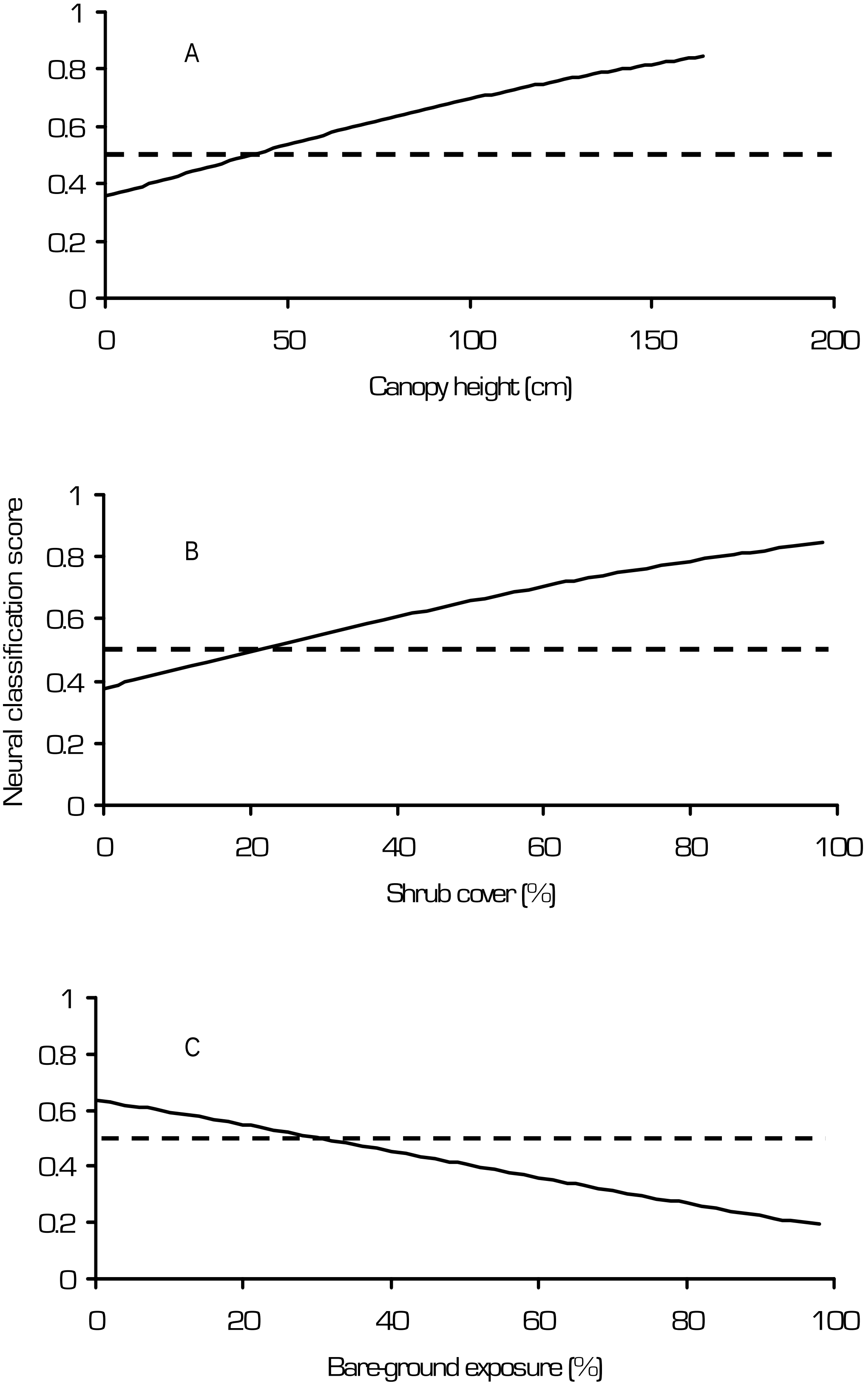
Fig. 2.3. Simulation results from the Swank and Gallizioli (1954) MLP model showing the predicted change in fall age ratio over the observed range of variation in total winter rainfall (cm). Data points represent observed fall age ratios. Inset: a diagrammatic representation of the 1-1-1 MLP used to model the data presented in Swank and Gallizioli (1954). The MLP contained 1 input node in the input layer (total winter rainfall), 1 neuron in the neuron layer, and 1 output node in the output layer (fall age ratio).


4
3.5
3
2.5
2
1.5
1
0.5
0
Predicted age ratio
0
10
20
30
40
Total winter (Dec–April) rainfall (cm)
Total winter rainfall
Neuron
Fall age ratio

sites and random locations and included vegetation canopy height (cm), percent cover by dominant tallgrass, percent cover by shrubs, bare ground exposure (%), and mean screening cover over 3 cover classes. The MLPs developed for this analysis contained 5 inputs, 2 neurons, and 1 output resulting in 15 parameters in the model. The output node represented nest sites and random locations and was coded 0.9 for nest sites and 0.1 for random locations. The network was trained with an adaptive learning rate for 500 iterations using a momentum of 0.8. The data were partitioned into training (88 cases) and validation (22 cases) sets before analysis. We measured accuracy using the area under the curve of the receiver operating characteristic (ROC) plot (Fielding and Bell 1997, Fielding 1999b). This method provides a threshold-independent method for measuring accuracy. However, for our graphical presentation of the results, we used an arbitrary threshold of 0.5 for discriminating nest sites from random locations. We report results here only for the 3 most important variables in the model (relevance > 10%).

The MLP accounted for 40.1% of the variation in the training data and 43.6% of the variation in the validation data. The area under the ROC curve was 0.842 for the training data and 0.768 for the testing data. That is, there was an 84.2% probability of correctly classifying a randomly selected pair of nest and random points based solely on the relative difference in their classification scores. The simulation analyses showed the change in suitability of a given location for use as a nest site as vegetation canopy height, percent cover by shrubs, and bare-ground exposure (relevance = 32.9%, 31.2%, and 26.9%, respectively) each varied while all other variables were held at the mean (Fig. 2.4). One of the important pieces of information revealed by the simulations is the transition points between suitable and unsuitable. At the Mesa Vista Ranch, locations with canopies >40 cm were suitable for nesting (Fig. 2.4a). Locations with shrub cover >20% were also suitable as nest sites (Fig. 2.4b). However, bare-ground cover in excess of 30% rendered a particular location unsuitable for nesting (Fig. 2.4c).

Fig. 2.4. Simulation results from the trained neural network model for differentiating random and nest locations based on vegetation characteristics on the Mesa Vista Ranch in Roberts County, Texas, 2001–2002. Results are presented only for variables with >10% contribution to the model's output: A) canopy height (cm), B) percent shrub cover, and C) bare-ground exposure (%). Dashed horizontal lines represent an arbitrary 0.5 cutoff threshold between suitable and unsuitable.


A
B
C
Neural classification score
0
0.2
0.4
0.6
0.8
1
0
50
100
150
200
Canopy height (cm)
0
20
40
60
80
100
Shrub cover (%)
Bare-ground exposure (%)

Caveats

Although we have attempted to discuss limitations and peculiarities of the MLP technique in the text, there are a few more considerations when using MLPs for predictive or discriminant analysis. First, although MLPs models can be used for statistical modeling, they lack a statistical background for ascribing confidence limits to their predictions. An approximation can be achieved via bootstrapping (M. T. Hagan, Oklahoma State University, Department of Electrical and Computer Engineering, personal communication), although this can be computationally intensive depending on the complexity of the neural model. Further, a trained neural network does not have an associated P–value, although some of the associated measures of accuracy (e.g., r^2) can have P–values associated with them. However, as many authors have pointed out, the rampant use of P-values in the scientific literature is often uninformative (Cohen 1994, Anderson et al. 2000).

The ability of a MLP to find patterns in noisy data is both a strength and a weakness of the technique. Because of the power with which they can find patterns, MLPs are sensitive to outliers in the training data. A MLP will learn the appropriate responses necessary to predict an outlier. However, this may weaken the model's ability to generalize when presented with new data. The MLP's response will be distorted by the outlier, resulting in inaccurate predictions. This is similar to the effect that outliers can have on the slope or intercept of a regression line. Therefore, screening outliers from training and validation data will increase the accuracy of the models predictions when presented with new data.

A related problem is that of overfitting (also called overtraining; Smith 1996:113-114). Overfitting occurs when model predictions match the observed data too closely, resulting in a reduction in the model's ability to generalize. Although other techniques, such as multiple regression, are also susceptible to overfitting, it is not as great a concern because these techniques are generally restricted to linear relationships (Smith 1996:114). The MLP technique is especially susceptible to overfitting because a MLP can approximate any function (Hagan et al. 1996), and can, therefore, map a dataset exactly.

There are 3 techniques to prevent overfitting. The easiest method is to gauge the MLP's accuracy in predicting the validation dataset. Since the validation data have not been used in model training, the MLP's ability to accurately predict validation data can indicate when the model has overfit the training data (an overfit MLP would show excellent performance on training data, but weak performance on validation data). Limiting the number of training iterations can also reduce the danger of overfitting, but there are no quantitative guidelines for this approach. Finally, MLPs lose power as the number of neurons, and hence the number of parameters, is reduced. So elimination of neurons in the presence of overfitting may result in an MLP that generalizes better.

Finally, ANN models are phenomenological models and provide no information on the underlying mechanisms. However, traditional regression and discrimination models usually suffer the same limitation. Researchers must develop hypotheses for experimentation and testing to confirm relationships discovered in any model. Further, although trained MLP models can produce accurate predictions, the model parameters (i.e., synaptic and bias weights) are not as readily interpretable as coefficients from a multiple regression equation. This has been referred to as a lack of transparency and, as such, MLPs are considered black-box models (Boddy and Morris 1999). We have described 3 methods for obtaining further biologically significant information from neural networks that can ameliorate this limitation. Furthermore, this lack of transparency is not as much an issue in management, where making accurate decisions and predictions may be paramount.

Management Considerations

We have described an alternative method of data analysis to traditional statistical techniques. Multi-layer perceptrons are non-parametric, can approximate linear and non-linear functions, are not constrained by multicollinearity, and can be used for both prediction and discrimination. In addition, MLPs can predict and discriminate simultaneously. Although an extremely powerful tool, the lack of transparency and parsimony has discouraged some researchers from applying the ANN technique to their data. We believe that this hesitancy is misplaced and hope that we have demonstrated not only the mechanics of the method, but also its usefulness. Neural network modeling offers not only a method for elucidating complex relationships from multivariate datasets, but also can serve as a basis for making more accurate and efficient management and conservation decisions.

CHAPTER 3

A NEURAL NETWORK MODEL FOR PREDICTING NORTHERN BOBWHITE ABUNDANCE IN THE ROLLING RED PLAINS OF OKLAHOMA[1]

Introduction

More accurate predictions of species abundance are necessary for management and conservation to be effectively implemented (Leopold 1933, Peters 1992, Schneider et al. 1992). Such predictions are increasingly important as human impacts on the environment increase. Artificial neural network (ANN) models are extremely powerful and allow the investigation of linear and non-linear responses. As such, ANN models offer ecologists a powerful new tool for understanding the ecologies of declining species, which can lead to more-effective management (Colasanti 1991, Edwards and Morse 1995, Lek et al. 1996, Lek and Guégan 1999).

Current applications of ANN models include statistical modeling (Smith 1996). In this capacity, ANN models have considerable advantages over traditional statistical models, such as regression. Artificial neural networks are extremely powerful due to their capacity to learn from the data used during training. Another advantage of ANN models over traditional models is that ANNs are inherently non-linear (Haykin 1999:2). Because most ecological phenomena are non-linear (Maurer 1999:110), this property of ANN models makes them more useful than standard statistical models that are often limited to linear relationships (Lek et al. 1996*b*). Even minor non-linearities in the response of one variable to another can reduce the

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[1] Lusk, J. J., F. S. Guthery, and S. J. DeMaso. 2002. A neural network model for predicting northern bobwhite abundance in the Rolling Red Plains of Oklahoma. Pages 345—355, in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, Editors, Predicting species occurrences: issues of accuracy and scale. Island Press. Covello, California, USA.

predictive power of traditional statistical techniques (Paruelo and Tomasel 1997). Neural networks also do not require any *a priori* knowledge of the nature of the relationship between predictor and response variables, which makes available non-linear methods cumbersome (Smith 1996:19-20). ANNs find the form of the response in the data presented to them and, as such, are not constrained to simple curves, as are curvilinear regression techniques (Pedhazur 1982:406, Smith 1996:20). Finally, ANN models are non-parametric (Smith 1996:20). Use of non-normal data for neural model development will not bias the results (Baran et al. 1996).

Much is known about bobwhite ecology, so it offers an effective means of evaluating the ANN technique and its applicability to management and conservation. Furthermore, an understanding of bobwhite climate relationships is an important component of management and conservation of bobwhites. Bobwhite abundance has declined over much of their range during the past several decades (Koerth and Guthery 1988, Brennan 1991, Church et al. 1993, Sauer et al. 1997). Bobwhite declines may be accelerated by climate change in some regions of their range (Guthery et al. 2000). Although we cannot manage the weather, we can factor in its effects when making management plans. By working in cooperation with state management agencies, the results of our research can be directly and immediately applied in the field, completing the research – management cycle (Hejl and Granillo 1998, Kochert and Collopy 1998, Young and Varland 1998).

We developed an artificial neural network model to investigate the influence of weather patterns on the abundance of northern bobwhites (*Colinus virginianus*; bobwhites hereafter) in a semi-arid region of western Oklahoma, United States. An understanding of the effects of weather on species abundances is warranted in the light of global climate change (Root 1993, Schneider 1993). We also sought to evaluate the ANN modeling technique. Specifically, we 1) compared ANN model output with that of a traditional multiple regression model, 2) determined which model was better using a sums of squares criterion (Hilborn and Mangel 1997), and 3) conducted simulation modeling using the ANN and regression models.

Methods

We modeled bobwhite abundance in the Rolling Red Plains ecoregion of Oklahoma. This ecoregion is in western Oklahoma, excluding the panhandle (Peoples 1991), and occupies 5.7 million ha. Mean annual precipitation is 58 cm (Oklahoma Climatological Survey, unpublished data).

Biologists from the Oklahoma Department of Wildlife Conservation counted bobwhites in each county in Oklahoma. Survey routes were established in typical quail habitat (Peoples 1991). Each 32-km route was surveyed twice annually beginning in 1991: once in August and once in October. Surveys were conducted either at sunrise or 1 hr before sunset. Total number of bobwhites observed per 32-km route was used as an index of bobwhite abundance. Although roadside counts such as these are prone to biases, these surveys are positively related to the fall harvest in Oklahoma ($r > 0.70$, S. DeMaso, unpublished data).

Artificial Neural Networks

Artificial neural networks are mathematical algorithms developed to imitate the function of brain cells for the study of human cognition (Hagan et al. 1996:1-8, Smith 1996:1, Haykin 1999:6-9). However, early techniques were handicapped by their inability to handle non-linear relationships (Hagan et al. 1996:1-4, Smith 1996:8). In the 1980s, neural network modeling experienced a renaissance of sorts with the development of a backpropagation algorithm (see below) that is capable of handling non-linear relationships (Smith 1996:20).

Because of their foundations in cognitive science, many of the terms used to describe aspects of ANNs are derived from neurobiology. What follows is a short explanation of the terminology of neural network modeling and a brief description of how a typical neural model works. A neural network typically consists of 3 layers: the input nodes, the neurons (also called hidden nodes or processing elements), and the output nodes. However, ANNs with more than one neuron layer are possible. Typically, each node in each layer is connected to each node in the previous layer by synapses (connection weights), and, as such, is termed fully connected

(Smith 1996:21). The synapses store the information learned by the model (Haykin 1999:2), and are analogous to regression coefficients (Heffelfinger et al. 1999). Each input node represents an independent variable. Values of input nodes are scaled so that they range between zero and one (Smith 1996:67). Each neuron processes the input nodes by computing a logistic function from the sum of the inputs:

$$g(u) = \frac{1}{1 + e^{-u}},$$

where u is the weighted sum of the inputs ($w_j x_j$) plus a bias weight (w_b):

$$u = w_b + \sum_{j=1}^{J} w_j x_j$$

(Smith 1996:40). The logistic function above is the most widely used, but is not the only function available (Smith 1996:35). The values calculated by the neurons, $g(u)$, are transferred to the output nodes. The output nodes perform a similar calculation and their output is detransformed to obtain a prediction of the independent variable (Smith 1996:22). In backpropagation ANNs, the error between the predicted output and the actual output is calculated and propagated back through the model where it is used to adjust the values of the synaptic weights according to one of a variety of learning rules (Hagan et al. 1996:11-40; Smith 1996:67). The adjustment of the synapses is termed learning (Smith 1996:59). This process continues iteratively, with synapses adjusted after each forward pass, and is termed training. With each iteration, the ANN learns more about the relationship between inputs and outputs and, therefore, the prediction error decreases. Training is stopped before the model maps the relationship between inputs and outputs exactly. When this occurs, the network is said to be over-trained and the model's predictive abilities are diminished when presented with novel data (Hagan et al. 1996:11-22, Smith 1996:113). The use of ANNs in the ecological sciences requires predictability, and there is a trade-off between model generality and accuracy of prediction.

Because ANN models begin training with randomly selected connection weights, the minimum error achieved by a network may not be the global minimum, but only a local minimum (Smith 1996:62). Therefore, there may exist an error minimum lower than the one achieved by the network. However, Smith (1996:62) reported that the probability of such local minima existing decreases as more neurons are added to the model. Determining the optimum number of neurons should, therefore, maximize the chances of finding the global minimum in the error surface.

Database Construction

Roadside quail counts were initiated in Oklahoma in 1991, and therefore, our database comprised the 1991 – 1996 bobwhite surveys. We averaged each year's August and October count for our models. The database also included weather and land-use data as independent variables. Weather data were obtained on CD-ROM from EarthInfo, Inc. (Boulder, Colorado). We extracted mean monthly temperature data for June, July, and August. Seasonal precipitation data were calculated from total monthly precipitation. We divided the year as follows: winter = December, January, and February; spring = March, April, and May; and summer = June, July, and August. Therefore, seasonal precipitation equaled total monthly precipitation averaged for each 3-mo period. We grouped climate data into these periods because they represent ecologically important phases of the bobwhite's life cycle (breeding, recruitment, and winter survival). We did not include any time lag for the effects of rainfall on quail abundance because other networks we developed indicated this lag effect was not important to model predictions (J. Lusk, unpublished data). We used weather stations closest to each survey route for obtaining weather data. As measures of land-use and human impacts, we used cattle density on nonagricultural lands (total head/km^2) and the proportion of county area in agricultural crop and hay production (hereafter, agricultural production). We selected these variables because they are likely to have the greatest effect on bobwhite abundance (Murray 1958, Roseberry and Sudkamp 1998). Bobwhite abundance in Florida varied directly with cultivated acreage and inversely with acreage grazed (Murray 1958). These land-use variables were determined at the county level and were extracted from the Oklahoma Department of Agriculture's annual crop statistics for each survey year in the database.

The final variable included in the data set was the number of bobwhites counted during the previous year's survey. The number of bobwhites present in 1 yr is dependent on the number of bobwhites present the previous year. Furthermore, survival and reproduction may be density dependent (Roseberry and Klimstra 1984).

ANN Construction, Training, and Validation

Network Architecture. We used a three-layered, backpropagation neural network. The network consisted of a layer of input nodes representing the independent variables, a layer of neurons, and an output node representing the dependent variable. Our model was fully connected (Smith 1996:21). We used a commercial neural-modeling software package (QNet for Windows, v97.02, Vesta Services, Winnetka, Illinois) for ANN development. Including too many neurons in the neuron layer may result in reduced prediction ability and including too few will limit the complexity the network can accurately learn (Smith 1996:120-123). Therefore, we determined the optimal number of neurons experimentally by training models in which the same data set and model parameters were used, but the number of neurons was varied. We developed models that contained 2 through 9 neurons. We limited the maximum number of neurons to the number of input variables in the model. We selected the model with best performance gauged as the correlation between the predicted counts obtained from the model and the actual counts in the validation data set.

Training Parameters. We used an adaptive learning rule during model training (Smith 1996). In addition, 3 parameters were adjusted to optimize model performance. These parameters were the number of iterations, the learning rate, and the momentum. The values we selected for the learning rate and momentum were within the range of those found to be most effective in a wide variety of neural network applications (Smith 1996:77-90). The number of iterations controls how long the model has to learn the pattern and relationships among the variables in the model. The larger the number of iterations, the more attempts the network has to minimize prediction errors. We trained our model for 10,000 iterations. We believed that 10,000 iterations would allow the network to find the error minimum and allow us to stop training if the network began to over-fit the data. The learning rate controls the magnitude of the corrections of the synaptic weights per iteration based on the direction and magnitude of the change in the prediction error during past iterations (Smith 1996:77). Selection of too small a learning rate will increase the number of iterations necessary to reach an error minimum. However, selection of too large a learning rate may make the network unstable, resulting in oscillations in the prediction error (Hagan et al. 1996:9-5). We used a learning rate of 0.05. The final network parameter was momentum. Momentum determines how many past iterations are used in determining synaptic-weight adjustments in the current iteration (Smith 1996:85-88). Momentum keeps the error corrections moving in the same direction along the error surface (Smith 1996:85). If a large momentum value is used, it will take longer for weight corrections to respond to changes in the prediction error. In other words, synaptic weight adjustments are based on the long-term trend in prediction error, and momentum determines the number of iterations used in determining the long-term trend. We used a momentum of 0.90. This momentum is appropriate for most types of models (Smith 1996:86).

Validation. To assess the predictive ability, accuracy, and reliability of our ANN model, we presented the trained model with data not used in network training. We created a validation data set by extracting 20% of the data from the original data set. Data were rank-ordered by the number of quail counted, and every 5th record was assigned to the validation data set. There were 98 records in the original database, resulting in 20 records in the validation data set. The systematic removal of the validation data allowed us to gauge the performance of the network over the entire range of the original bobwhite count data. Because the validation data were derived from the original data set and were, therefore, obtained under the same conditions as those used for network training, the network can be considered only validated for this particular ecoregion in Oklahoma (Conroy 1993, Conroy et al. 1995).

In addition to our validation data set, we tested our model with data collected in the same ecoregion but not part of the training or validation data sets. Because this model will eventually be used by managers to predict bobwhite abundance, this test will determine the utility of the model. We presented the trained model with the 1997 data and recorded the accuracy of the predictions.

Regression Analysis

We performed a multiple regression analysis to compare ANN performance with that of this traditional statistical model. We used the same data set used for training and validating the ANN model for the regression analysis. The full-model, multiple linear regression included all the independent variables and the dependent variable used in the ANN model. We used the statistical software package Statistix (Analytical Software 1996). We used the Student's *t*-test for determining which variables were contributing ($P < 0.05$) to the model predictions (Analytical Software 1996). The correlation between each model's predicted and actual bobwhite count was used as an indicator of the relative performance of each model.

Model Comparison

We used the percent contribution of each variable to the ANN model's predictions to identify important variables (Özesmi and Özesmi 1999). The percent contribution is calculated by dividing the sum-of-squared synaptic weights for the variable of interest by the total sum-of-squared synaptic weights for all variables. For the regression model, we determined each variable's contribution to the total, unadjusted R^2 using a forward stepwise regression (Wilkinson 1998). We calculated the increase in R^2 after each variable was entered into the model to apportion the amount of variance accounted for to each variable. We then divided each individual R^2 by the total unadjusted R^2 for the model. This gave the percentage contribution of each variable in the regression model to the model's response. This percentage is, therefore, homologous to the percent contribution of the ANN model. Although these percentage contributions are not directly comparable, they allowed us to determine what variables were driving each model.

To determine if the differences in performance were due to the increased power of the ANN modeling technique, or to the increased parameterization of the ANN model, we used a sum-of-squares criterion for model comparison (Hilborn and Mangel 1997:114-117). This technique adjusts the sum of squared deviations (SS) by penalizing parameterization:

$$\mathrm{SS}_{\mathrm{a}} = \frac{\mathrm{SS}_{\mathrm{m}}}{(n-2m)},$$

where 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 1997:115). This sum-of-squares criterion is similar to Mallow's C_p (Hilborn and Mangel 1997:116). As such, the model with the lowest adjusted sum-of-squares is selected as the best predictor of the dependent variable (Hilborn and Mangel 1997:116). The SS deviations for each model were calculated from the observed and predicted values of the bobwhite counts. We calculated the SS from the training data only, resulting in an n of 78. The ANN model had 34 parameters (one for each synapse: nine inputs x three neurons = 27, an additional three synapses connecting each of the neurons to the output node, and four bias weights, one for each neuron and output node), and the regression model had ten parameters (regression coefficients, one for each independent variable, and the constant).

Simulation Analyses

Following model training and validation, we used simulations to explore the effects of each independent variable on ANN model predictions (Lek et al. 1996*a*, Heffelfinger et al. 1999). This allowed us to further evaluate model performance. We constructed simulation data sets in which 1 independent variable was allowed to vary incrementally between its maximum and minimum value and all other variables were held constant at their mean value.

These data sets were then processed through the trained neural network to generate predicted bobwhite counts. Predicted counts were then plotted against the range of the variable allowed to vary to determine the response of network predictions to that particular variable.

Results

We determined that 3 neurons were optimal for the data set. The ANN model accounted for 78% (R^2) of the variation in bobwhite counts in the training data and 32% of the variation in bobwhite counts in the validation data (Fig. 3.1). The lower R^2 for the validation data resulted mainly from a single outlier (Fig. 3.1). With this outlier removed, the amount of variation accounted for by the ANN model increased to 52%. However, we could find no reason for the large prediction error associated with this data point and so provide both results here. Our test of the network model accounted for 17% of the variation in the 1997 data ($R^2 = 0.17$). The full-model regression was not significant and accounted for 6% of the variation in bobwhite counts ($F_{9,68} = 1.50$; $P = 0.17$; Fig. 3.2). The regression model accounted for 37% of the variation in the validation data set ($R^2 = 0.37$; Fig. 3.2). The sum-of-squares criterion indicated that the regression model ($SS_A = 223.3$) was the better predictor of bobwhite abundance than the ANN model ($SS_A = 282.1$; Table 3.1). In other words, the increased predictive power of the ANN model was not enough to warrant increased complexity.

Although it is not possible to determine statistically the significance of the variables in the ANN model, we assume that the importance of independent variables is related to the magnitude of its contribution to predictions. Each of the independent variables contributed some information to the model predictions (Table 3.2). Mean August temperature and summer precipitation had the highest individual contributions to the network outputs, with a combined contribution of 32% (Table 3.2). The remaining variables also contributed to the ANN model's predictions, but to a lesser extent (Table 3.2). There was one variable significant

Table 3.1. Parsimony analysis of the artificial neural network model and the regression model using the adjusted sum-of-squares (Hilborn and Mangel 1997).

Model	Number of Parameters	Sum-of-squares	Adjusted Sum-of-squares
Artificial Neural Network	34	2,821.64	282.1
Regression	10	12,950.90	223.3

Table 3.2. Contribution of each independent variable to the artificial neural network and regression models' predictions of bobwhite abundance in the Rolling Red Plains of Oklahoma.

	Neural Network	Regression model		
Independent variable	Percent contribution	Percent contribution[a]	t	P
Mean June temperature (C)	12.5	2	-0.75	0.4568
Mean July temperature (C)	13.5	1	-0.31	0.7540
Mean August temperature (C)	16.0	5	0.57	0.5702
Winter precipitation (cm)	12.5	54	2.30	0.0245
Spring precipitation (cm)	7.0	15	-1.47	0.1462
Summer precipitation (cm)	16.0	9	-1.06	0.2913
Proportion cropland[b]	7.0	3	0.14	0.8928
Cattle density[c]	7.5	0	0.17	0.8637
Previous year's bobwhite count	8.0	11	1.57	0.2218

[a] Individual R^2 expressed as a percent of the total R^2 (0.166) accounted for by the model.

[b] Proportion of county area in agricultural production.

[c] Total head per hectare of non-agricultural land.

Figure 3.1. Predicted bobwhite counts from the artificial neural network model plotted against the actual values in the (a) training data set and (b) the validation data set, for the Rolling Red Plains of western Oklahoma. The trend line represents the linear model regression of predicted bobwhite count on the actual bobwhite count.

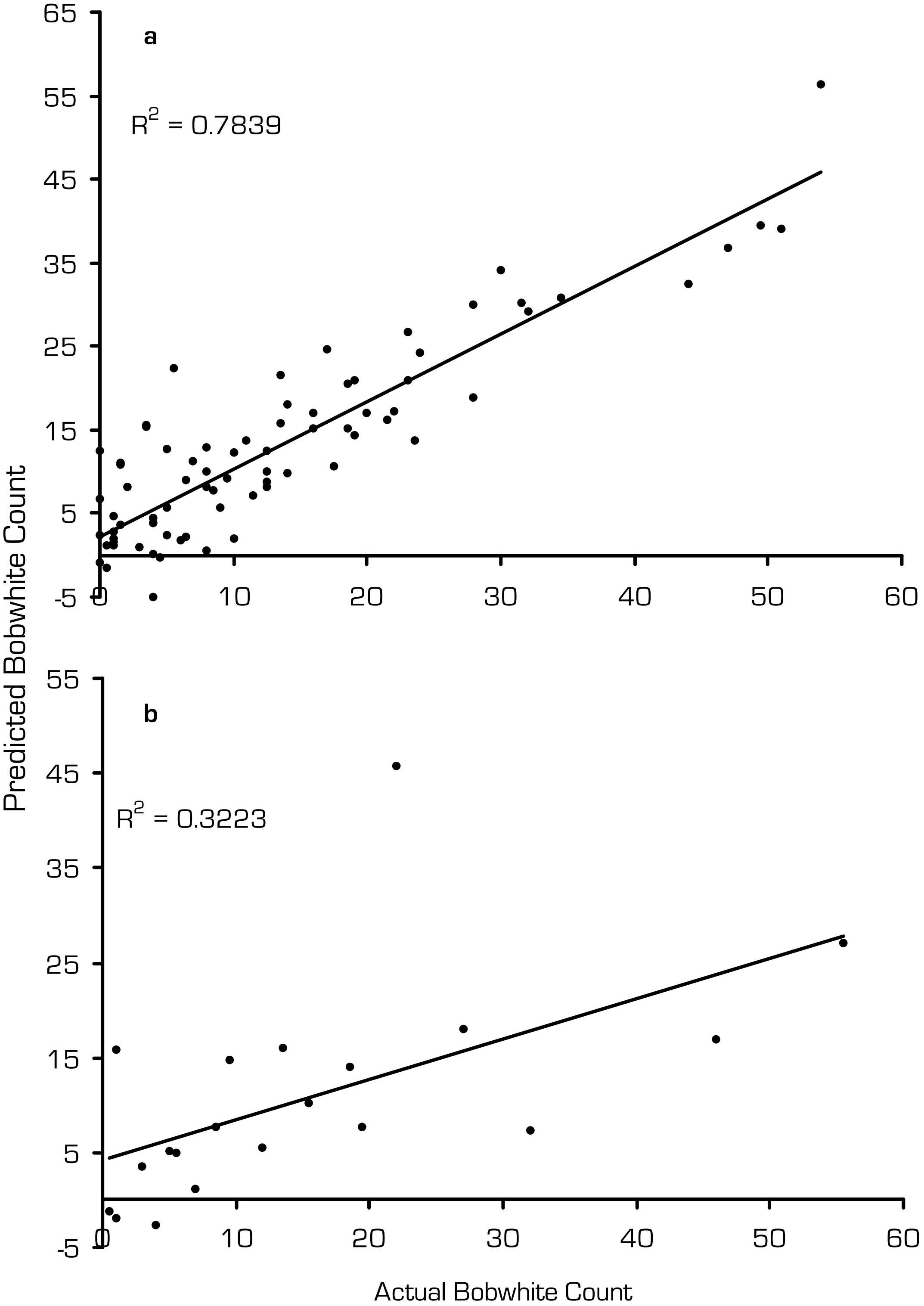
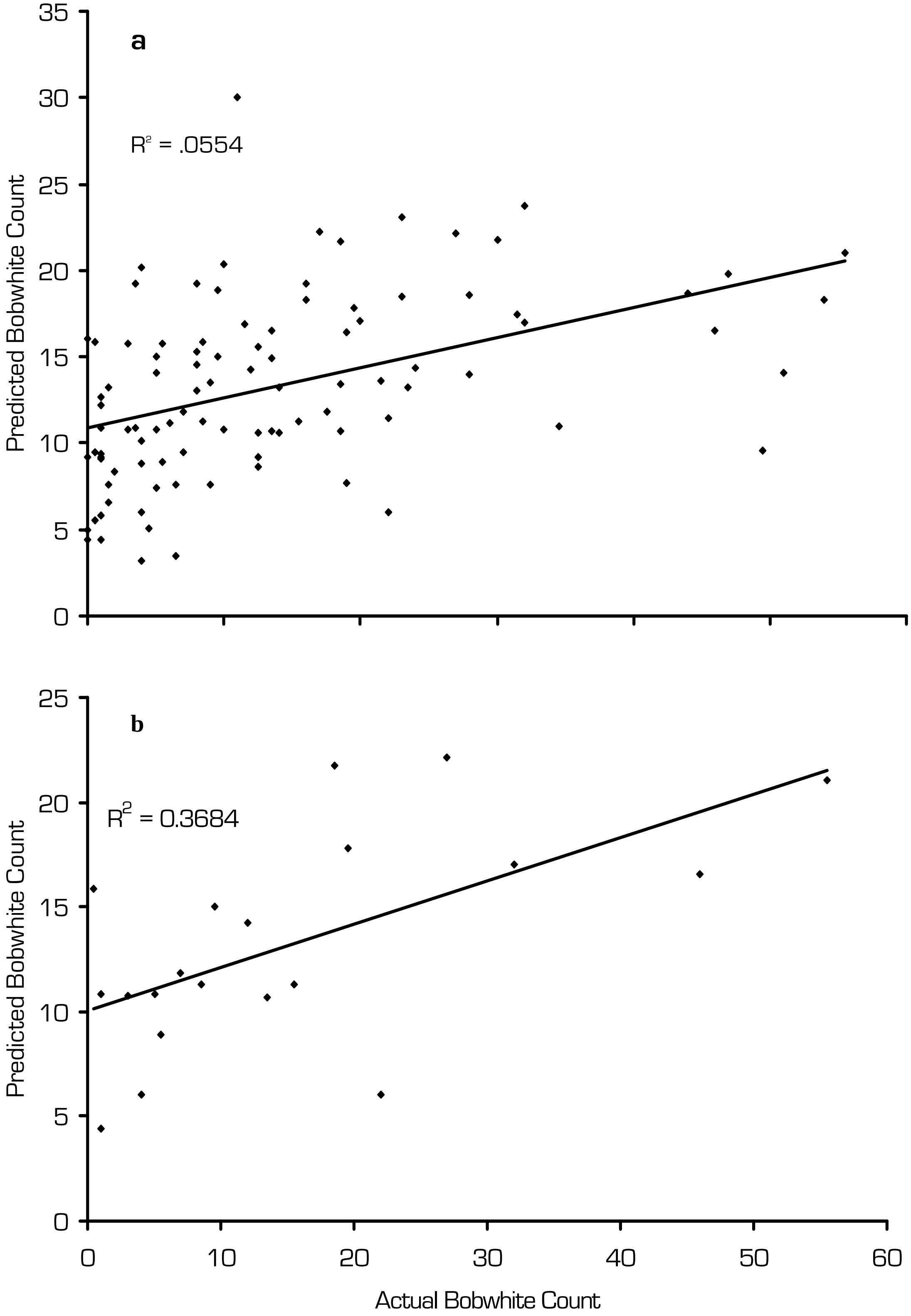

a
R^2 = 0.7839
b
R^2 = 0.3223
Predicted Bobwhite Count
Actual Bobwhite Count
65
55
45
35
25
15
5
-5
0
10
20
30
40
50
60

Figure 3.2. Predicted bobwhite counts from the full model regression plotted against the actual values in (a) “training” data set and (b) the validation data set, for the Rolling Red Plains of western Oklahoma. The trend line represents the linear model regression of predicted bobwhite count on actual bobwhite count.


a
R² = .0554
Predicted Bobwhite Count
35
30
25
20
15
10
5
0
b
R² = 0.3684
Predicted Bobwhite Count
25
20
15
10
5
0
0
10
20
30
40
50
60
Actual Bobwhite Count

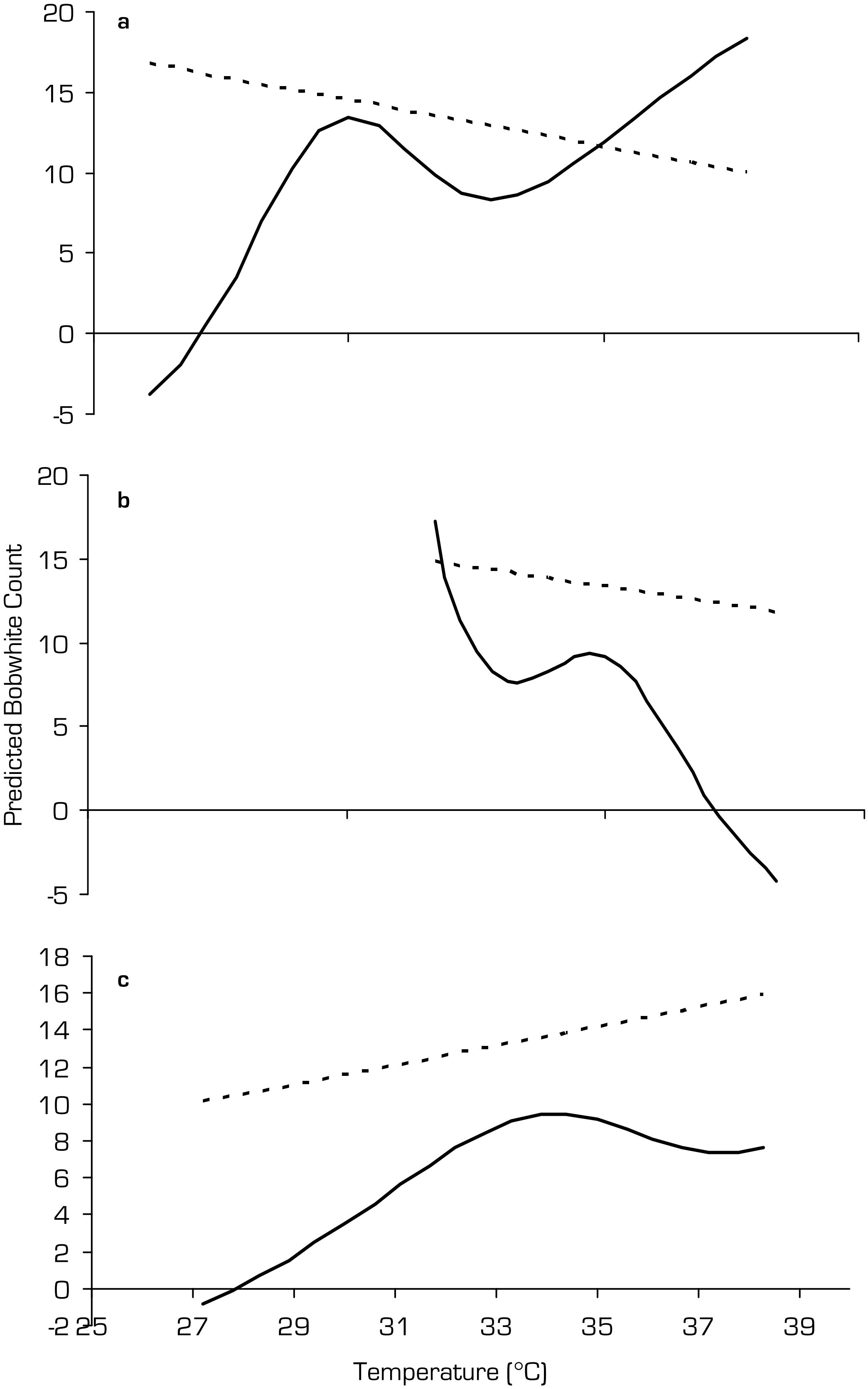
for the regression model: winter precipitation (Table 3.2). Winter precipitation also accounted for 54% of the total R^2 of the regression model (Table 3.2). Only spring precipitation and the previous year's bobwhite counts contributed more than 10% to the overall R^2 (15% and 11%, respectively; Table 3.2). The density of cattle on non-agricultural land contributed nothing to the overall R^2.

The Student's t-test we used to determine significant variables in the regression model was limited to linear relationships. Such linear relationships did not exist for all variables as indicated by the ANN model. Predicted bobwhite counts increased non-linearly with increasing June and August mean monthly temperature. Predicted bobwhite counts increased with increasing June temperature until approximately 30 C, after which, predicted counts decreased (Fig. 3.3a). Predicted counts also increased with increasing August temperature until approximately 34 C, after which predicted counts also decreased (Fig. 3.3c). The regression model predicted a steadily decreasing count with increasing June temperatures, and a steadily increasing bobwhite count with increasing August temperatures (Figs. 3.3a and 3.3c, respectively). As July temperature increased, the ANN model predicted bobwhite counts decreased non-linearly. However, the regression model predicted bobwhite counts would not respond strongly to July temperature, although the regression predictions did decrease with increasing July Temperature (Fig. 3.3b).

There was a near-linear relationship between winter precipitation and bobwhite counts as predicted by the ANN model (Fig. 3.4a). The regression model predicted a positive linear relationship (Fig. 3.4a). Increases in winter precipitation increased bobwhite counts, but counts decreased with both spring and summer precipitation (Figs. 3.4b and 3.4c, respectively). These predictions matched those of the regression model, in that they predicted decreases. However, the ANN model suggested non-linearities in the responses.

Predicted bobwhite counts reached their maximum value at mid-levels of the proportion of county area in agricultural production and the number of bobwhites counted

Fig. 3.3. Neural network simulation analyses (solid line) and regression predictions (dashed line) of the response of bobwhite counts in the Rolling Red Plains of western Oklahoma to mean monthly temperature in (a) June, (b) July, and (c) August. Temperature is reported in degrees Celsius, and the same scale was used for each plot.



a
20
15
10
5
0
-5
b
20
15
10
5
0
-5
Predicted Bobwhite Count
c
18
16
14
12
10
8
6
4
2
0
-2
25
27
29
31
33
35
37
39
Temperature (°C)

Figure 3.4. Neural network simulation results (solid line) and regression predictions (dashed line) of the response of bobwhite counts to seasonal precipitation in the Rolling Red Plains of western Oklahoma. Winter months (a) included December, January, and February; spring months (b) included March, April, and May; and summer months (c) included June, July, and August. Precipitation is reported in centimeters, but each plot has its own scale.

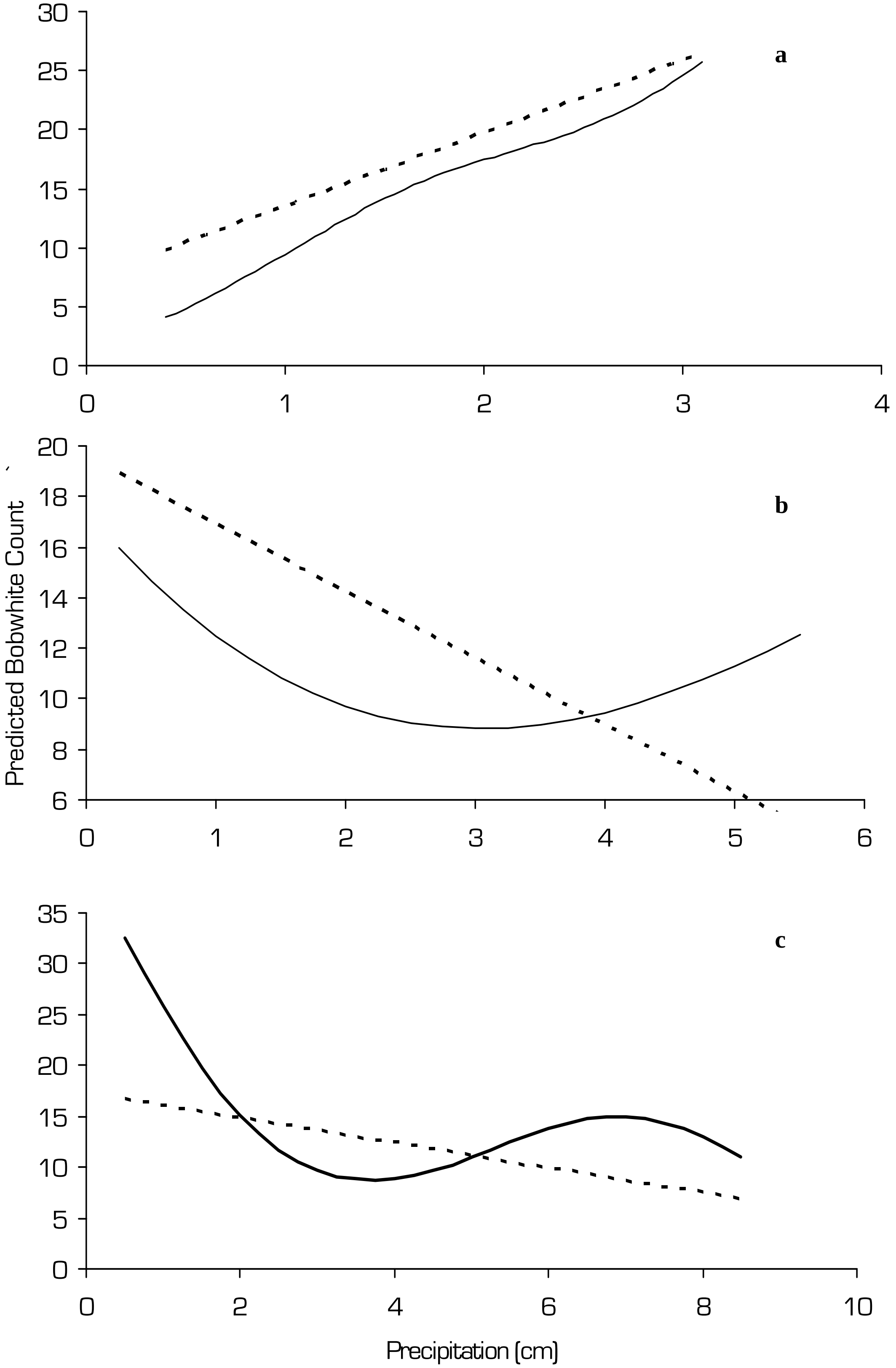
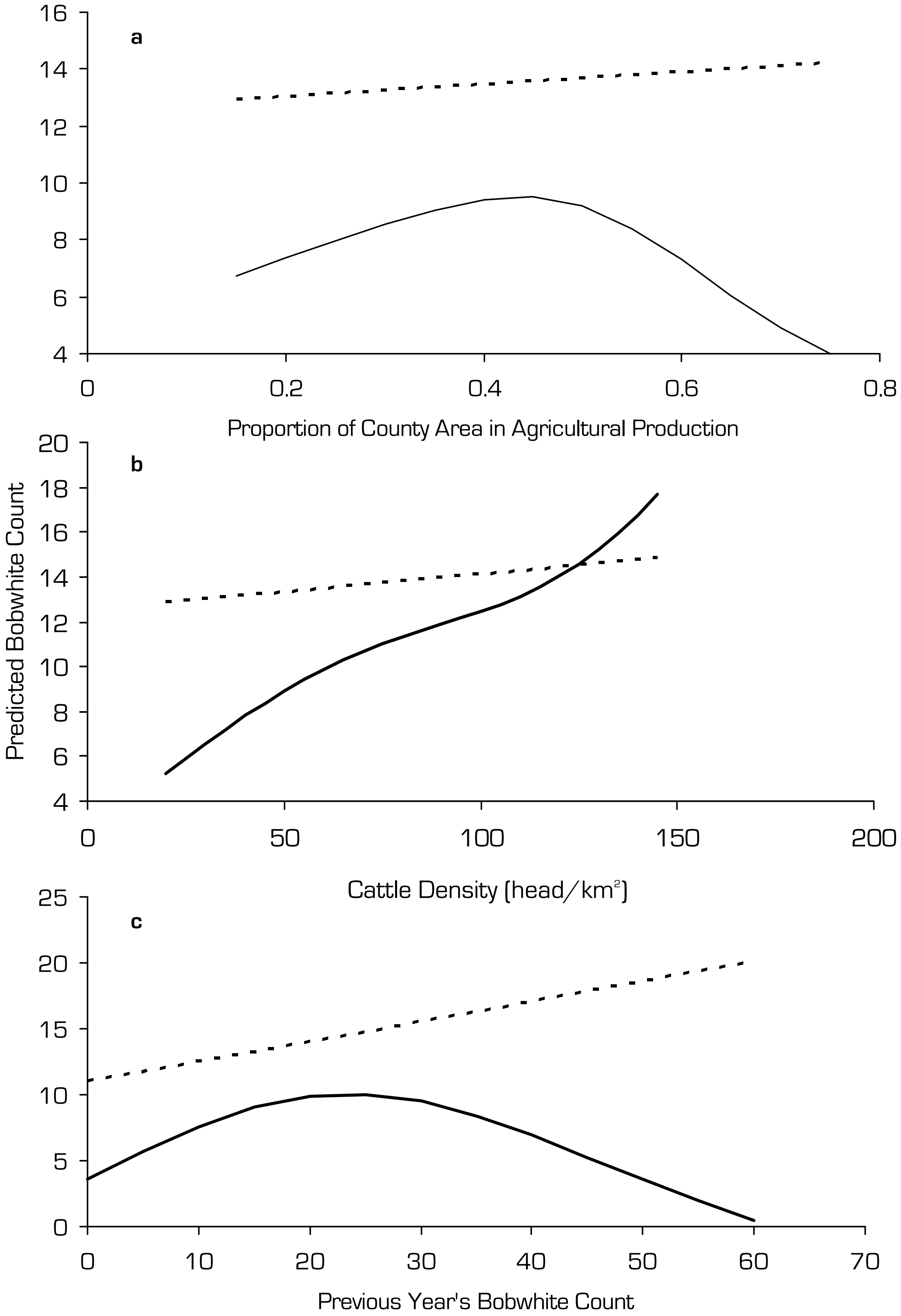

30
25
20
15
10
5
0
0
1
2
3
4
a
20
18
16
14
12
10
8
6
0
1
2
3
4
5
6
b
Predicted Bobwhite Count
35
30
25
20
15
10
5
0
0
2
4
6
8
10
c
Precipitation (cm)

Figure 3.5. Neural network simulation results (solid line) and regression predictions (dashed line) of the response of bobwhite counts in the Rolling Red Plains of western Oklahoma to (a) the proportion of county area in agricultural production, (b) cattle density on non-agricultural lands, and (c) the previous year's bobwhite count. Cattle density is reported as total number of head per km^2 of non-agricultural land.


a
16
14
12
10
8
6
4
0
0.2
0.4
0.6
0.8
Proportion of County Area in Agricultural Production
b
20
18
16
14
12
10
8
6
4
0
50
100
150
200
Cattle Density (head/km²)
Predicted Bobwhite Count
c
25
20
15
10
5
0
0
10
20
30
40
50
60
70
Previous Year's Bobwhite Count

during the previous year's survey (Figs 3.5a and 3.5c, respectively). The regression model predicted little response of bobwhite counts to the proportion of county area in agriculture, but there was a positive trend (Fig. 3.5a). The regression model also predicted a linear increase in bobwhite counts with increasing previous year's counts (Fig. 3.5c). Predicted bobwhite counts also increased near-linearly with increasing cattle density, although the regression model showed little effect of cattle density on bobwhite counts (Fig. 3.5b).

Discussion

The application of ANN modeling techniques to the study of ecological phenomena has great potential for understanding complex, dynamic processes (Colasanti 1991, Edwards and Morse 1995, Lek et al. 1996*b*). However, to date, little research has made use of this tool. When applied to an ecological research problem, ANN models have consistently out-performed traditional statistical models (Recknagel et al. 1997, Maier et al. 1998). Artificial neural networks have proved highly effective in predicting aboveground biomass in the tallgrass prairie (Olson and Cochran 1998). Compared to regression models, ANNs predicted biomass and described changes in standing biomass with substantially greater accuracy. Heffelfinger et al. (1999) used ANNs to accurately predict call counts and age ratios for Gambel's quail (*Callipepla gambelii*) in Arizona from precipitation and temperature data. Other studies have used ANNs to accurately predict trout (*Salmo trutta*) abundance (Baran et al. 1996, Lek et al. 1996*a*). Mastrorillo et al. (1997) used a neural model to correctly predict the presence of three small-bodied fish in freshwater streams in >80% of cases. Özesmi and Özesmi (1999) compared ANNs with logistic regression to classify locations in a GIS database as nest or non-nest sites for red-winged blackbirds (*Agelaius phoencieus*) and marsh wrens (*Cistothorus palustris*) based on site characteristics. Their ANN models out-performed logistic regressions in all but one case. The better performance of the ANN model resulted because nest-site selection by these marsh-nesting species was a non-linear process.

For our data set, the regression model performed better than the ANN model based on the adjusted sum-of-squares criterion. Our neural model also performed poorly when presented with 1997 data, but the weather in 1997 was outside the range of conditions used to train the model. We have found that the magnitude of deviations from long-term mean conditions may have a greater effect on bobwhite populations than yearly weather conditions (Lusk et al. 2001). This may in part be responsible for the network's poor performance in 1997. However, the additional knowledge gained by using the ANN modeling technique is essential for successful management. Management and conservation decisions based on incomplete or misleading information can only harm the species of concern. Simplicity is only one criterion by which to judge a model's performance. Also important is the ability of the model to approximate the process under investigation (Burnham and Anderson 1998:23). The ANN model provided more biologically meaningful predictions of responses, because the ANN was able to find the non-linear elements of the responses. We believe that the length of the data set may have limited our results. The six years for which we have data may not have sufficiently captured the response of bobwhites to climate variables. Dynamics in semiarid areas are characterized by episodic events that require long-term data. Model accuracy is a function of sample size (Smith 1996:134). Furthermore, with small sample sizes, such as those used in our study, the effects of noise on the model's performance is amplified, especially if the relationship being modeled is complex (Smith 1996:115). Too small of a sample size can reduce the ability of the ANN model to generalize, but there are no sample-size restrictions to the application of neural networks (Paruelo and Tomasel 1997).

Using simulations (Lek et al. 1996*a*, Heffelfinger et al. 1999, Özesmi and Özesmi 1999), ANN models provide information on the effects of the independent variables on bobwhite abundance. This provides not only a better understanding of bobwhite ecology, but also allows us to evaluate the ANN model's explanatory ability. June, July, and August temperatures were important contributors to the model's predictions (Table 3.2); however, August temperature contributed more than June or July temperatures. The higher importance of August temperature may be an artifact of counting quail in the fall. Because climate conditions can affect the daily activity patterns of bobwhites (Roseberry and Klimstra 1984), conditions during the roadside counts may have a larger influence on the network's predictions. This influence is the result of the more direct effect of the conditions during the count on the count's outcome. Our model predicted that bobwhite abundance would increase with June and August temperature, but only to a certain temperature, after which counts declined. The increase in counts predicted at high June temperatures is probably the result of too few data points in that part of the range, making the predictions susceptible to outliers. Had we limited our simulation data set to within 1 sd of the mean, the effects of outliers may have been reduced. Predicted bobwhite counts decreased with increasing July temperature. Summer heat decreased California quail (*Callipepla californica*) chick survival in California (Sumner 1935). Quail productivity was negatively associated with summer temperature in northwest Florida (Murray 1958), and July-August temperature was negatively associated with the length of the nesting season and positively associated with nest abandonment in southern Illinois (Klimstra and Roseberry 1975). July temperature decreased the age ratios of Gambel's quail in Arizona (Heffelfinger et al. 1999). Bobwhites in Texas avoided habitat space-time (Guthery 1997) in which the operative temperature was >39 C (Forrester et al. 1998).

Our ANN model indicated a near-linear, positive relationship between winter precipitation and predicted bobwhite counts. This near-linearity probably accounts for the significance of this variable in the regression model (Table 3.2). Winter precipitation may indirectly influence bobwhite abundance through increased spring vegetation, seed, and insect production (Swank and Gallizioli 1954, Sowls 1960). Scaled quail (*Callipepla squamata*) abundance in Texas (Giuliano and Lutz 1993) and bobwhite harvest in Illinois (Edwards 1972) were strongly, positively correlated with January-March precipitation. Spring and summer precipitation had negative curvilinear relationships with bobwhite abundance. Among gallinaceous birds, young are susceptible to precipitation for the first few days of life (Newton 1998) and increased rain early in the hatching season may lead to increased juvenile mortality

(Sumner 1935). Although most studies of the effects of spring precipitation on quail abundance report a non-significant relationship (e.g., Campbell 1968, Campbell et al. 1973, Heffelfinger et al. 1999), spring rain might affect breeding behavior adversely, therefore, reducing fall abundance.

Similar to the findings of Roseberry and Sudkamp (1998), our model predicted bobwhite abundance to be greatest at intermediate levels of agricultural land use. As agricultural land increases, initially there may not be a net loss of usable space-time for quail. Bobwhite abundance at low proportions of agricultural use may result from an abundance of mid- to late-successional habitat, less suitable for bobwhites. Similar to the intermediate disturbance hypothesis (Connell 1978), intermediate levels of agriculture may provide bobwhites with more of the habitat components necessary to support large populations than less agriculturally developed lands. Other research has indicated that bobwhites are associated with patchy heterogeneous landscapes with moderate levels of grassland, row crop, and woody edge (Roseberry and Sudkamp 1998). However, as the proportion of agricultural land increases, there is a net loss of usable space-time, any further edge becomes redundant (Guthery and Bingham 1992), and quail abundance declines.

Predicted bobwhite counts increased with increasing cattle density. This is counter to other research that indicates grazing negatively influences quail habitat (Schemnitz 1961). However, Spears et al. (1993) found that site productivity governs the seral stage most important to bobwhites. Early successional stages are favorable for bobwhites on more productive sites, whereas late seral stages are favorable on less productive sites. Because western Oklahoma is semi-arid, and therefore, less productive, the positive response we found (Fig. 3.5b) is not consistent with expectations.

Predicted bobwhite abundance showed a weak but discernible density-dependent effect in relation to the previous year's bobwhite count. For bobwhite counts higher than approximately 25, predicted counts for the next fall decreased. The implication of this result is that at current levels of habitat space-time availability, bobwhite abundances above a certain level will adversely affect the population as a whole. In other words, the available habitat space-time can only support a given number of bobwhites, regardless of climate conditions beneficial to bobwhite increase.

Conclusions

We believe ANN modeling techniques offer wildlife managers and conservationists with a valuable and powerful tool for managing species of concern. Although the ANN model did not outperform the regression model based on the adjusted sum-of-squares criterion, the ANN model did provide a better understanding of how bobwhite abundances in the Rolling Red Plains of Oklahoma respond to climate and land-use variables. Non-linear relationships, although widespread in nature, are often ignored by researchers (Gates et al. 1994). The ability of the ANN technique to find the non-linear responses of quail abundance to climate variables makes ANN models preferred to traditional linear and non-linear techniques, that require the specification of the curvilinear response variable. A lack of knowledge of the ecologies of many species makes specification of the correct polynomial term a matter of trial and error.

Model validation indicated that the ANN technique was accurate for this region of Oklahoma, but the increase in power was only due to the increased parameterization of the ANN model. However, use of linear modeling techniques may result in a misunderstanding of the factors influencing a particular process. Our regression analysis was only able to identify the linear relationship between winter rain and bobwhite abundance. Any management or conservation plan must take into account climatic factors if it is to be successfully implemented. Furthermore, the ANN model we described can continue to learn as more data become available, and can, therefore, be used as part of an adaptive management plan (Morrison et al. 1998). Our analysis was limited to a 5-yr data set that may not have represented the entire spectrum of response by bobwhites to climate variables. The predictions of the simulation analyses can be used to generate hypotheses suitable for empirical testing (Recknagel et al. 1997). Simulations also can be used to judge the biological realism of the ANN predictions and increase the understanding of the factors influencing a species' abundance. The use of ANN models also can allow more cost-effective management because the data used to generate the predictions are readily available and cheaply obtained. Our model will be used by the Oklahoma Department of Wildlife Conservation to estimate bobwhite abundances for the management of the fall harvest. A similar modeling effort is underway for Texas Parks and Wildlife Department. We will develop a model that will be used by managers in better managing bobwhites in Texas.

CHAPTER 4

NORTHERN BOBWHITE (*COLINUS VIRGINIANUS*) ABUNDANCE IN RELATION TO YEARLY WEATHER AND LONG-TERM CLIMATE PATTERNS[1]

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 8 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 4-neuron network was

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[1] Lusk, J. J, F. S. Guthery, and S. J. DeMaso. 2001. Northern bobwhite (*Colinus virginianus*) abundance in relation to yearly weather and long-term climate patterns. Ecological Modelling 146: 3—15.

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 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.

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 behavior 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).

Methods

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%/year (Church et al., 1993; Sauer et al., 1997). However, the rate of decline accelerated between 1982 and 1991 to 3.5%/year (Church et al., 1993). In Oklahoma, the long-term rate of decline has not been as severe, averaging only 0.20%/year (Sauer et al., 1997), but during the period between 1993 and 1996, the rate of decline in Oklahoma accelerated to 7.36%/year (Sauer et al., 1997).

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 hr 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 all routes. 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.

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 ≥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 2 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.

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 approximately 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).

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 3 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 2 and 9 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 2 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 validations data subset.

Neural networks were trained for 5,000 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 (SS_A) is calculated as:

$$SS_a = \frac{SS_m}{(n - 2m)},$$

where 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.

Results

Neural Models

A network with 8 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 4.1). The single greatest contributor to the weather network's predictions was cattle density on non-cultivated land (18%, Table 4.1).

A 4-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 4.1). Deviations from mean total winter, spring, and summer precipitation contributed 42.8% to the network's predictions (Table 4.1).

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

Table 4.1. Independent variable contributions to neural network predictions of normalized bobwhite counts (1991-1997) in Oklahoma based on weather and climate data. Percent contribution reflects the importance of a particular variable in determining a neural network's predictions relative to other variables.

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 (mean maximum temperature, mean total precipitation) 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 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.

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.

Simulation Analyses

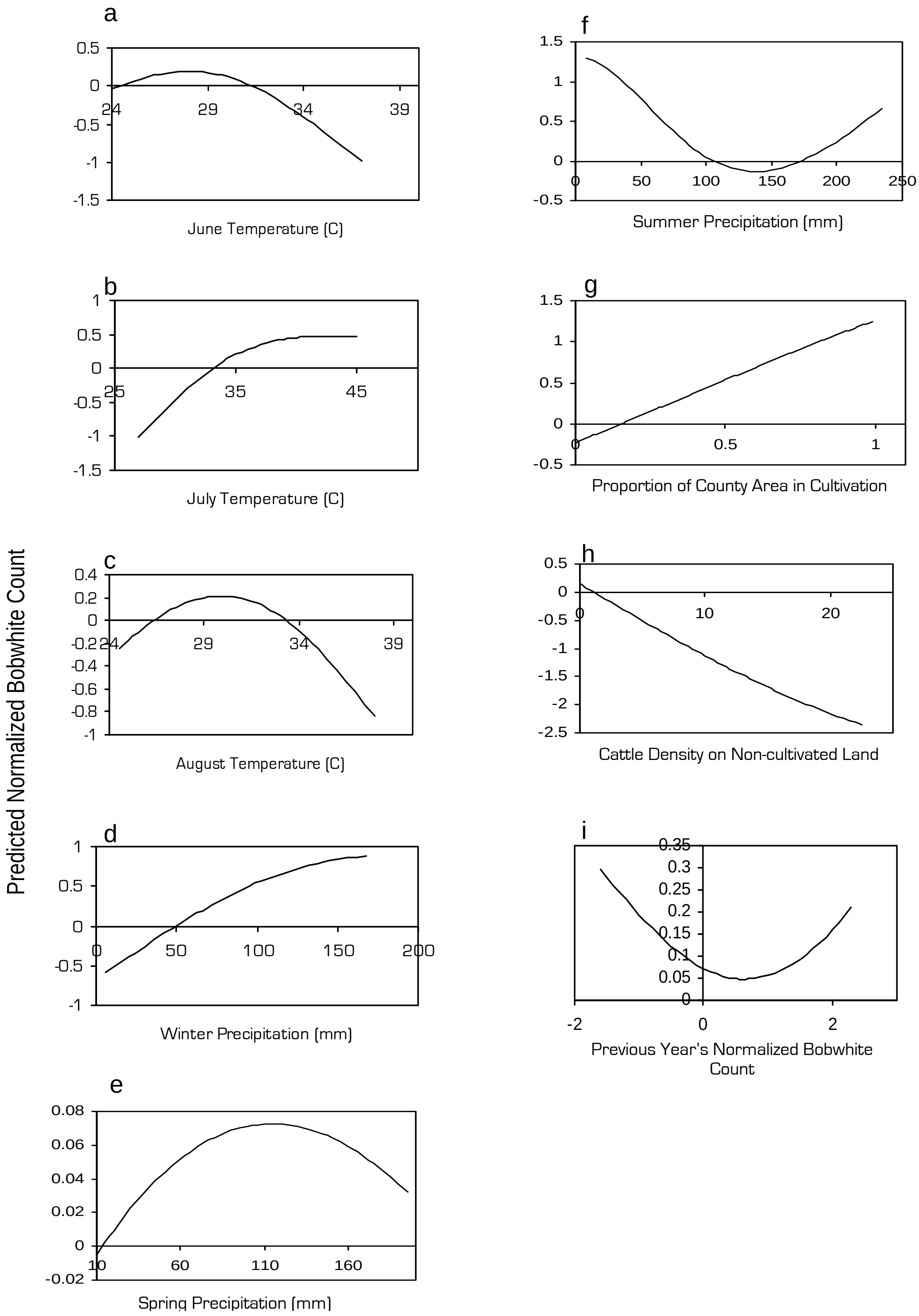
Although all variables contributed to network predictions, some variables had relatively minor contributions. For our weather network, spring precipitation and last year's normalized counts both contributed <10% (Table 4.1). We therefore restrict our discussion to the remaining variables for the weather simulations. However, we provide the simulation results for the low-contribution variables in Figure 4.1.

As June temperature increased past approximately 31°C, the weather network predicted that bobwhite counts will be less than the route mean (Fig. 4.1a). Below this temperature, counts were predicted to be slightly more than the route mean (Fig. 4.1a). An opposite trend was observed for July temperature (Fig. 4.1b). 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. 4.1b). 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 approximately 26°C and above approximately 33°C (Fig. 4.1c).

The weather network's predictions for winter precipitation indicated that counts continued to increase above the mean as precipitation increased above 50 mm (Fig. 4.1d). The effects of summer precipitation showed counts above the mean, except when precipitation was between approximately 110 and approximately 170 mm (Fig. 4.1f).

Land-use variables contributed substantially to the network's predictions (Table 4.1). The weather network predicted that bobwhite counts that were greater than the mean count

Fig. 4.1. 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) mean maximum temperature; winter (d), spring (e), and summer (f) mean total 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).


Predicted Normalized Bobwhite Count
a
0.5
0
-0.5
-1
-1.5
24
29
34
39
June Temperature (C)
b
1
0.5
0
-0.5
-1
-1.5
25
35
45
July Temperature (C)
c
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
24
29
34
39
August Temperature (C)
d
1
0.5
0
-0.5
-1
0
50
100
150
200
Winter Precipitation (mm)
e
0.08
0.06
0.04
0.02
0
-0.02
10
60
110
160
Spring Precipitation (mm)
f
1.5
1
0.5
0
-0.5
0
50
100
150
200
250
Summer Precipitation (mm)
g
1.5
1
0.5
0
-0.5
0
0.5
1
Proportion of County Area in Cultivation
h
0.5
0
-0.5
-1
-1.5
-2
-2.5
0
10
20
Cattle Density on Non-cultivated Land
i
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
-2
0
2
Previous Year's Normalized Bobwhite Count

when the proportion of area in cultivation exceeded 0.15 (Fig. 4.1g), 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. 4.1h).

Like the weather network, some variables in the climate model contributed relatively little to the network's predictions (Table 4.1). 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 Figure 4.2.

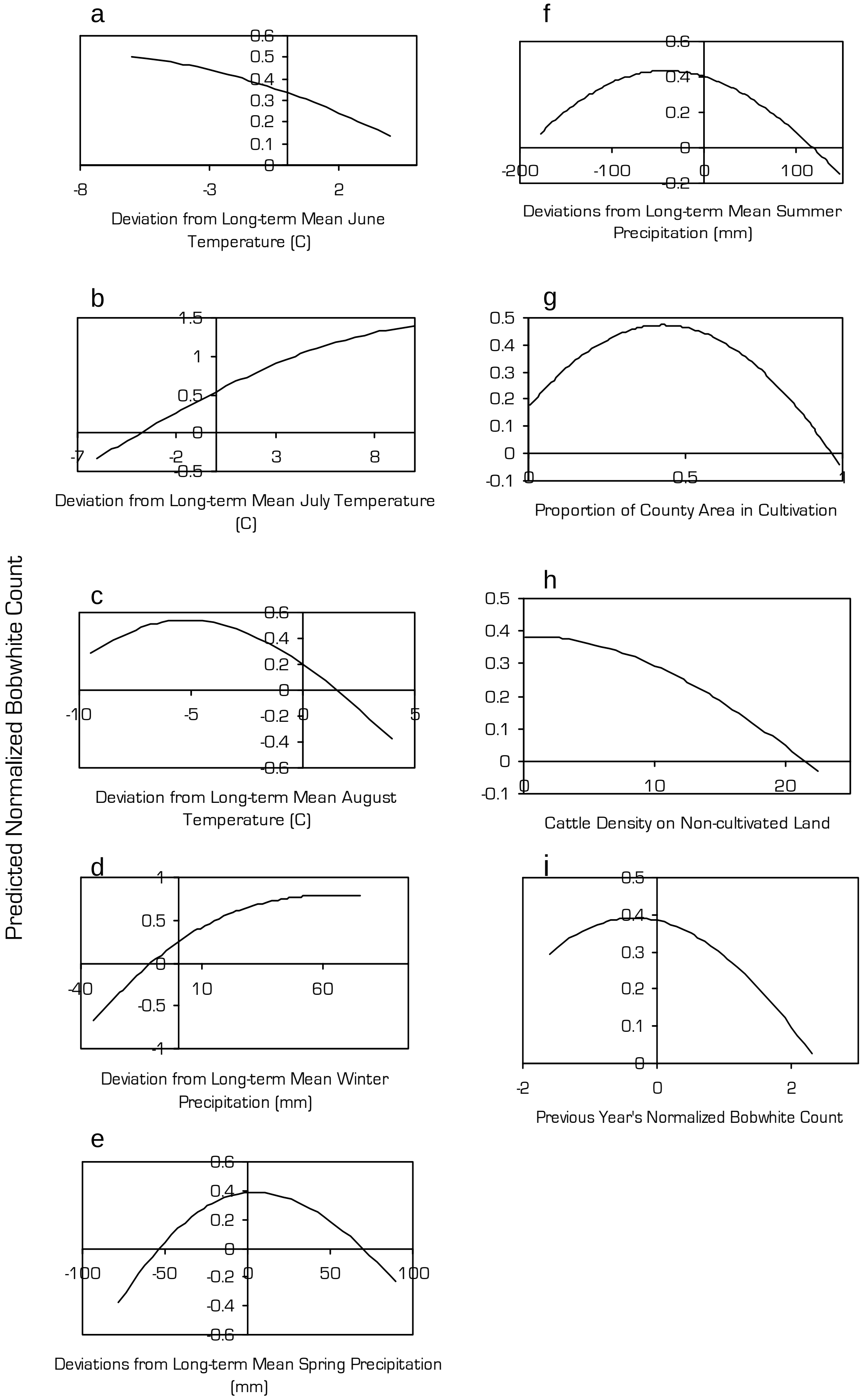
Positive deviations of July temperature from the long-term mean resulted in higher bobwhite counts (Fig. 4.2b). Predicted counts did not fall below the mean counts until temperature deviated more than −4°C from normal (Fig. 4.2b). However, August temperatures below the mean resulted in increased predicted bobwhite counts and temperatures above the mean by more than 2°C resulted in below average counts (Fig. 4.2c).

Positive deviations from long-term winter precipitation resulted in predicted counts above the mean (Fig. 4.2d). Counts did not fall below the mean until precipitation fell 30 mm below normal (Fig. 4.2d). Above-average counts were predicted over a wide range of deviations from mean spring rain, but were highest near the mean (Fig. 4.2e). 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. 4.2f). However, the peak increase in predicted counts occurred when rain was approximately 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.

Discussion

Climate changes predicted by the current generation of simulation models, if accurate, will undoubtedly have consequences for wildlife species in almost every ecosystem.

Figure 4.2. 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) mean maximum temperature; deviation from long-term mean winter (d), spring (e), and summer (f) mean total 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).


Predicted Normalized Bobwhite Count
a
0.6
0.5
0.4
0.3
0.2
0.1
0
-8
-3
2
Deviation from Long-term Mean June Temperature (C)
f
0.6
0.4
0.2
0
-0.2
-200
-100
0
100
Deviations from Long-term Mean Summer Precipitation (mm)
b
1.5
1
0.5
0
-0.5
-7
-2
3
8
Deviation from Long-term Mean July Temperature (C)
g
0.5
0.4
0.3
0.2
0.1
0
-0.1
0
0.5
1
Proportion of County Area in Cultivation
c
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-10
-5
0
5
Deviation from Long-term Mean August Temperature (C)
h
0.5
0.4
0.3
0.2
0.1
0
-0.1
0
10
20
Cattle Density on Non-cultivated Land
d
1
0.5
0
-0.5
-1
-40
10
60
Deviation from Long-term Mean Winter Precipitation (mm)
i
0.5
0.4
0.3
0.2
0.1
0
-2
0
2
Previous Year's Normalized Bobwhite Count
e
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-100
-50
0
50
100
Deviations from Long-term Mean Spring Precipitation (mm)

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, 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 approximately 31°C and August temperatures higher than approximately 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, 2000), 32°C in Sonora, Mexico, and 29°C in Arizona, USA (Guthery, 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 (Kilmstra and Roseberry, 1975), and female bobwhites stop laying at high temperatures (Guthery, 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 later 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.

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.

CHAPTER 5

RELATIVE ABUNDANCE OF BOBWHITES IN RELATION TO WEATHER AND LAND USE[1]

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 (December—February), spring (March—May), summer (June—August), and fall (September—November) rainfall. We also included the proportion of county area in cultivation, the number of livestock per hectare of non-cultivated 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.

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[1] Lusk, J. J., F. S. Guthery, R. R. George, M. J. Peterson, and S. J. DeMaso. 2002. Relative abundance of bobwhites in relation to weather and land use. Journal of Wildlife Management 66: 1040—1051.

Although many relationships appeared approximately linear or were decelerating, proportion of county area in cultivation and livestock density on non-cultivated 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.

Introduction

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), non-catastrophic 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 can also affect bobwhite production (Leopold 1933, Robinson and Baker 1955, 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, Guthery et al. 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 non-linear 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 be indicative of a lack of a relationship between the variables. Second, non-linear 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 non-linear, 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, Inc., 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 the years 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 kph, 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 ≥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 non-cultivated 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, 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.

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 (Özesmi and Özesmi 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 5.1) 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 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.

Table 5.1. State- and ecosystem-level means for independent variables used to develop a predictive model for northern bobwhite abundance in Texas, 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 non-cultivated land.

Results

A 4-neuron model was optimal for the overall data set and explained 65% of the variation in the training data (Fig. 5.1a) and 61% of the variation in the validation data (Fig. 5.1b). The variables most important to the network's predictions (relevance >10%) were July temperature, fall rainfall, livestock density on non-cultivated land, and the previous year's bobwhite count (Table 5.2). The proportion of county area in cultivation was also important, but its relevance score was below (9.3%; Table 5.2) our arbitrary 10% cutoff point. The remaining variables also influenced the index of abundance, but to a lesser extent (see Discussion). We report, therefore, 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. 5.2a). 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 mean maximum July temperature (Fig. 5.2b). 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. 5.2c). 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.

Table 5.2. Relevance (importance) of input variables in a 4-neuron neural model developed to predict the abundance of northern bobwhites in Texas 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 non-cultivated land.

Fig. 5.1. Predicted versus observed northern bobwhite counts recorded by Texas Parks and Wildlife Department biologists during annual August 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.

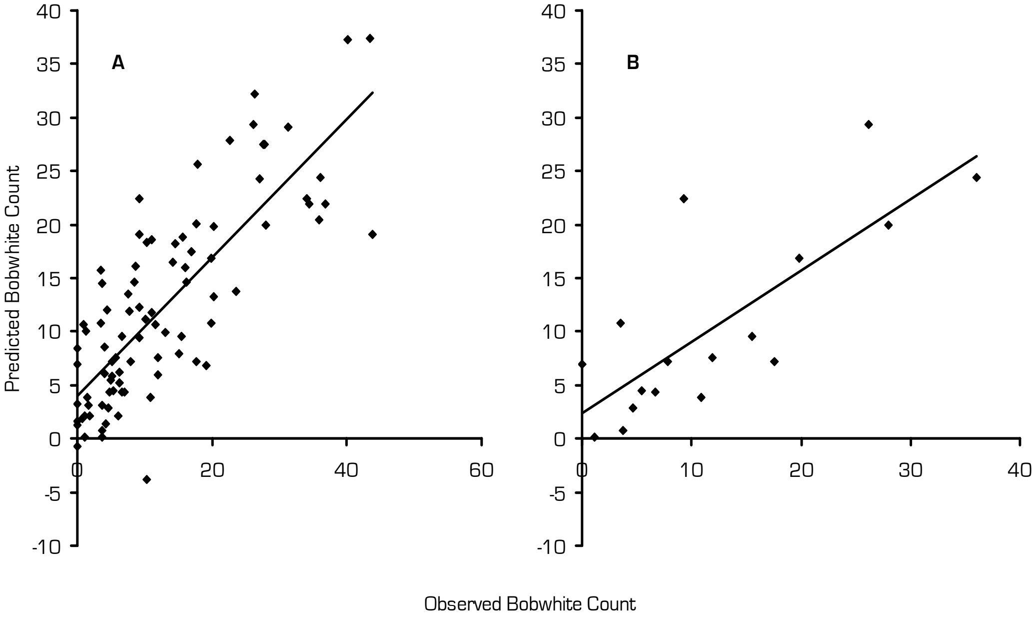

A
B
Predicted Bobwhite Count
Observed Bobwhite Count
40
35
30
25
20
15
10
5
0
-5
-10
0
20
40
60
0
10
20
30
40

Fig. 5.2. Predicted northern bobwhite counts from simulation analyses of the effects of June (A), July (B), and August (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 5.1). 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.

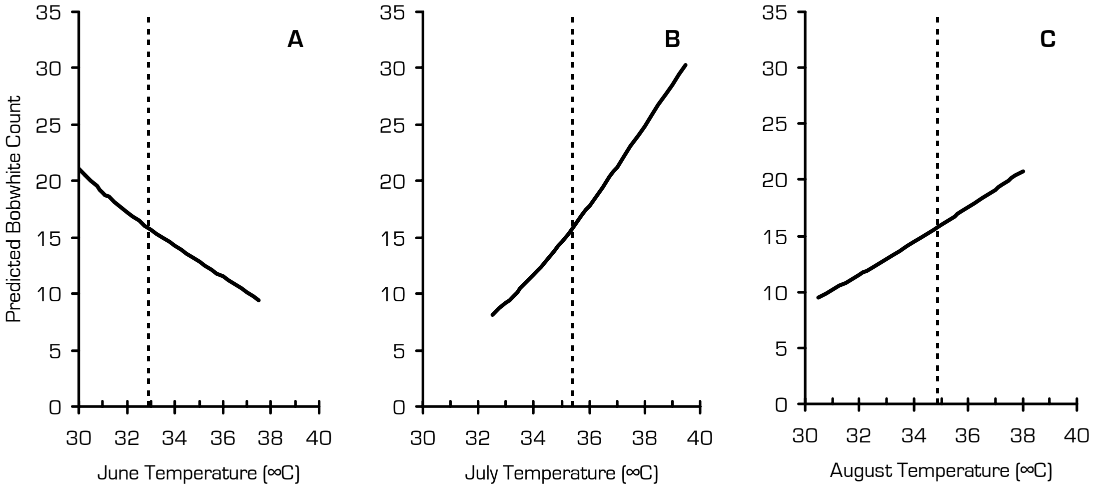
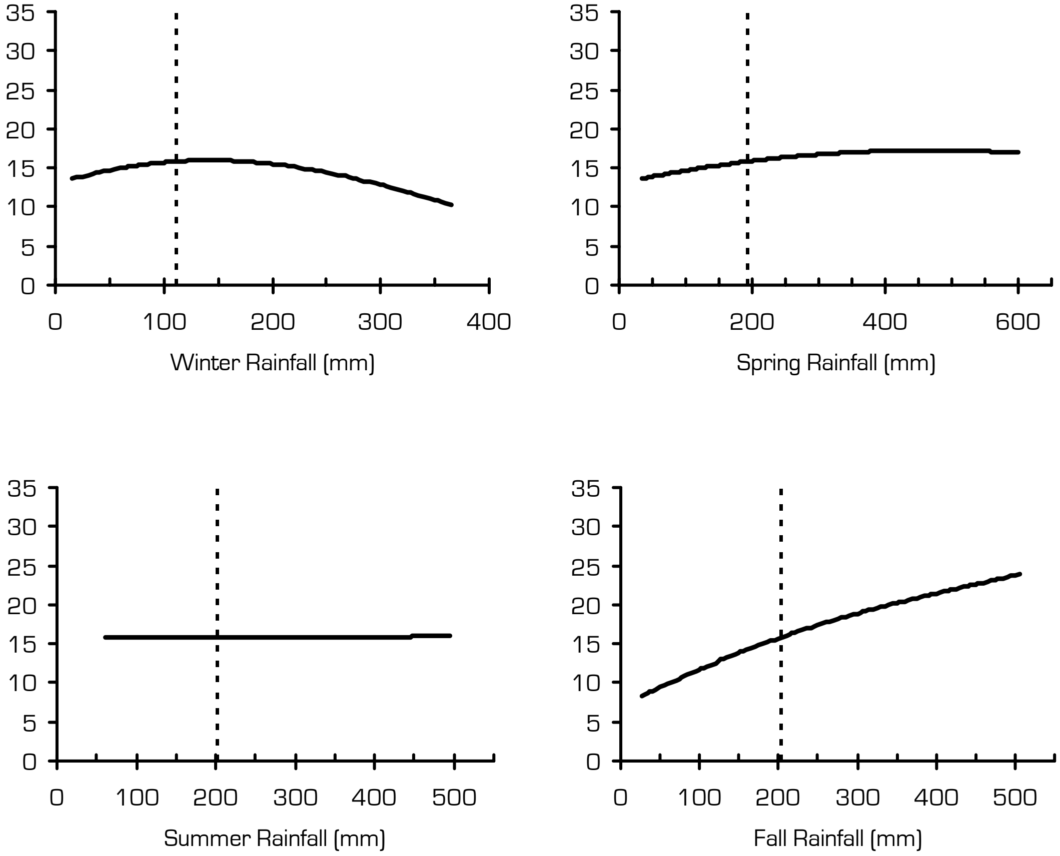

A
B
C
Predicted Bobwhite Count
35
30
25
20
15
10
5
0
30
32
34
36
38
40
June Temperature (∞C)
July Temperature (∞C)
August Temperature (∞C)

Fig. 5.3. 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.

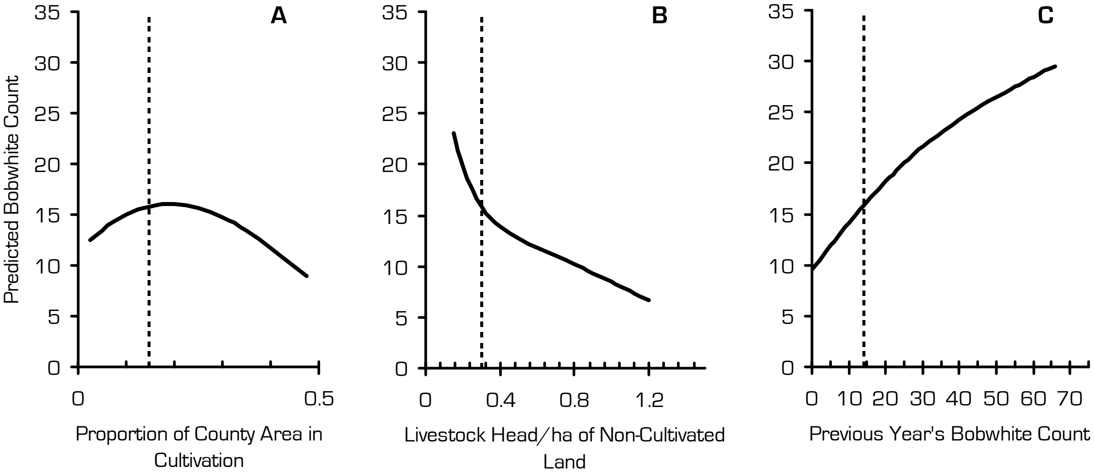

35
30
25
20
15
10
5
0
0
100
200
300
400
Winter Rainfall (mm)
35
30
25
20
15
10
5
0
0
200
400
600
Spring Rainfall (mm)
35
30
25
20
15
10
5
0
0
100
200
300
400
500
Summer Rainfall (mm)
35
30
25
20
15
10
5
0
0
100
200
300
400
500
Fall Rainfall (mm)

The network predicted that increases in winter rainfall were non-linearly related to the bobwhite index, although the effect was slight (Fig. 5.3a). The bobwhite index was unresponsive to either spring (Fig. 5.3b) or summer (Fig. 5.3c) rainfall in our simulations. Increasing fall rainfall resulted in increased bobwhite counts, but the relationship was slightly decelerating (Fig. 5.3d). 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. 5.4a), 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 non-cultivated land were followed by declines in the index (Fig. 5.4b). 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. 5.4c), 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,

Fig. 5.4. 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 non-cultivated 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 5.1). 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.


A
B
C
Predicted Bobwhite Count
35
30
25
20
15
10
5
0
0
0.5
Proportion of County Area in Cultivation
0
0.4
0.8
1.2
Livestock Head/ha of Non-Cultivated Land
0
10
20
30
40
50
60
70
Previous Year's Bobwhite Count

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 means in the Gulf Prairies, Edwards Plateau, and the High Plains. Comparing means for the 5 most important variables in the model (Tables 5.1 and 5.2) 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 5.1). 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. 5.3d). 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 non-cultivated land (Fig. 5.4b). 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. 5.4b), 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 insured that the network we obtained made the best compromise between bias and variance (Lek et al. 2000).

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 as 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 the current 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, where 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 is also 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 5.1), 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 5.1) 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. As 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.

CHAPTER 6

EFFECT OF CLIMATE DEVIATIONS ON NORTHERN BOBWHITE ABUNDANCE IN TEXAS[1]

Introduction

Climate and weather patterns can both affect the abundance of a species (Chapter 4). The relative importance of each factor, however, can determine how a species in a particular locale will respond to climate change. Some weather conditions might be physiologically intolerable for the species (Dawson 1992, Dunham 1993), especially those species that exist near the upper limits of their thermal tolerances in certain portions of their range (Tracy 1992). However, if a species has adapted to local conditions, deviations from the normal conditions might have a more important effect on abundance. Therefore, a change in mean annual temperature of 1-4 °C (Peters 1992, Schneider 1993) might affect populations in different portions of the species' range differently. In some areas, depending on the seasonality of the temperature shift and its magnitude in the region (IPCC 1998), the actual deviation from normal conditions might be small, resulting in minor changes in species abundance. However, the magnitude of the temperature changes in North America are expected to be at least 40% greater than the global average (IPCC 2001)

Here I model the effects of deviations from long-term climate conditions on bobwhite abundance in Texas. I compare the results of this model with those reported in Chapter 5 on the effects of weather and land use on bobwhite abundance.

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[1] This chapter is intended to provide a compliment to Chapter 4's analysis of the relative effects of climate and weather in Oklahoma for the analysis of abundance in relation to weather in Texas (Chapter 5).

Methods

Bobwhite abundance data were obtained from Texas Parks and Wildlife Department (TPWD) for 1978 through 1997. These data were collected annually during the first 2 weeks of August along permanently marked 32.2-km routes (Perez 1998, Chapter 5). The total number of bobwhites observed at 1.6 km intervals along the routes was recorded. I used routes from ecoregions (Gould 1975) in which bobwhites had a consistent presence over the period of study. That is, there was at least one non-zero count along each route contained in the final dataset. Raw counts from each route within ecoregions were averaged for each year. This composite index of bobwhite abundance was used as the dependent variable in the model (Chapter 5).

Weather data were obtained from the National Oceanic and Atmospheric Administration's National Climate Data Center (EarthInfo, Boulder, Colorado, USA). Weather stations closest to the starting point of each survey route were selected for inclusion in the database. I determined proximity using the latitude and longitude coordinates of the weather stations and survey routes, and included a weather station only if it was within 1 ° of latitude and longitude, and if the weather records were ≥90% complete. June, July, and August mean maximum temperature and total winter, spring, summer and fall precipitation were extracted from the data for each year and route. To estimate deviations from long-term climate conditions, I averaged the weather data over the entire period of record (range: 30-100 years) for each weather station in the database. The yearly weather values were then subtracted from the long-term averages and the differences were averaged within ecoregions for each year, to match the indices of bobwhite abundance. These deviations were then used as predictor variables in the neural model.

Also included in the database were 2 variables describing land use: proportion of cultivated land and the number of livestock per hectare of uncultivated land within the county through which each survey route passed. I obtained the crop and livestock statistics from the Texas Department of Agricultural Statistics. Cropland was summed over each county and averaged within each ecoregion for each year. Livestock densities were treated in an analogous manner. However, as reported in Chapter 5, livestock data were unavailable for 1988 through 1992. Again, these years were not included in the final database, as a result. The final variable in the model was the index from the previous year's count for each ecoregion. This variable accounted for density dependence in bobwhite abundance.

I used a 3-layer network architecture and developed the neural model using Statistica's Neural Networks (SNN; StatSoft, Tulsa, Oklahoma, USA). See Chapter 2 for a detailed description of neural modeling architecture used in this chapter. The database contained 10 independent variables (7 climate, 2 land-use, and 1 population). These data were partitioned into training and validation data subsets. Training data were comprised of 80% of the original data, and were used to adjust the synaptic weights during training (Smith 1996). The testing and validation data were comprised of the remaining 20% of the original data, and were used as a diagnostic against overfitting and for measuring the accuracy of the model when presented with novel data (Rykiel 1996, Fielding 1999). The testing data were not used to adjust the synaptic weights.

The modeling procedure varied somewhat from that used in Chapter 5. Statistica's Neural Networks carries out many of the training procedures automatically. Using the thorough search method, SNN examined all possible combinations of independent variables and number of neurons, and selects the best performing model based on predictive performance and model complexity. Therefore, the final model included only those variables that significantly improved model performance. The variables included in the model are ranked by importance to model predictions based on relevance scores. These scores are calculated as the sum of the squared synaptic weights of the variable of interest divided by the sum of squared synaptic weights for all variables in the model (Özesmi and Özesmi 1999).

I used simulations to interpret model output (Lek et al. 1996). Simulation data were generated in SNN by allowing the variable of interest to vary incrementally between its maximum and minimum values while holding all other variables constant at their mean value.

These data were then processed using the model and the predicted abundance was plotted against the variable of interest. These response curves showed how abundance responded to variation in a particular independent variable.

I compared the performance of the climate model with the performance of the weather model reported in Chapter 5 using the adjusted sum-of-squares method. The adjusted sum-of-squares divides the model sum-of-squares (SS_m) by the sample size (n), reduced by 2x the number of parameters (m):

$$SS_a = \frac{SS_m}{(n - 2m)}$$

This method corrects the sum-of-squares for the level of parameterization and allowed me to compare models with different numbers of parameters (Hillborn and Mangel 1997). The model with the lowest adjusted sum-of-squares is the best-performing model after accounting for parameterization (Hillborn and Mangel 1997).

Results

The best model for predicting bobwhite abundance contained 5 neurons and 3 input variables, and accounted for 49.5% of the variation in the data (Fig. 6.1). The variables included in the model included the previous year's bobwhite count (relevance = 61.6%), deviation from long-term mean June temperature (relevance = 27.8%), and livestock density on noncultivated land (relevance = 10.6%).

The unadjusted, model sum-of-squares for the climate model was 5473.8 and for the weather model reported in chapter 5 it was 4037.2. The weather model had an adjusted sum-of-squares of 576.74 and the climate model reported here had an adjusted sum-of-squares of 146.97. Therefore, the climate model was the better predictor of bobwhite abundance than the weather model (Chapter 5).

Predicted bobwhite count was a decelerating positive function of the previous year's count (Fig. 6.2). Predicted counts increased rapidly in a nearly linear fashion with increasing previous year's count until previous year's count reached approximately 15 bobwhites, at

Fig. 6.1. Predicted versus observed bobwhite abundance for counts recorded by Texas Parks and Wildlife Department during annual August surveys (1978—1997) for both training and testing datasets combined using a 5-neuron neural network.

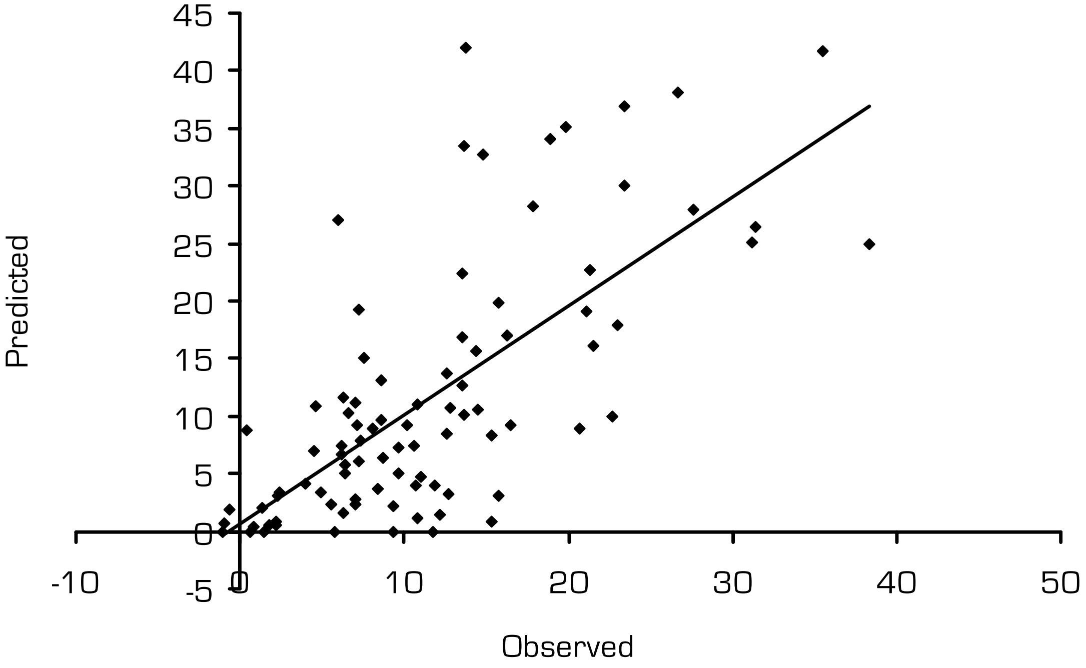
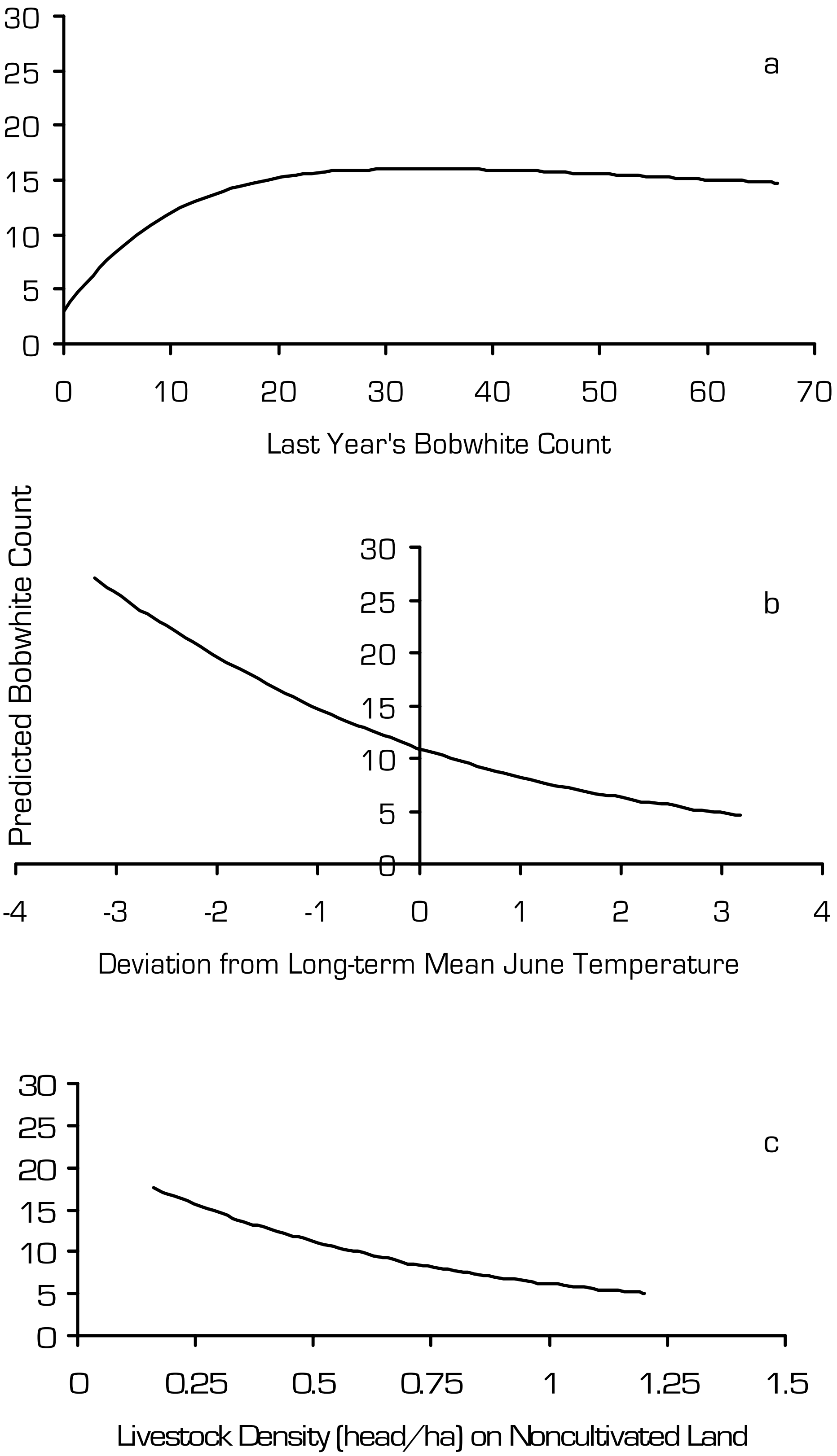

45
40
35
30
25
20
15
10
5
0
-5
-10
0
10
20
30
40
50
Predicted
Observed

Fig. 6.2. Predicted bobwhite abundance as a function of (a) the previous year's bobwhite count, (b) deviations from long-term mean June temperature, and (c) livestock density on noncultivated lands generated by the 5-neuron neural network. The variable of interest was varied incrementally from the maximum observed value to the minimum observed value while the remaining variables were held constant at their means. The scale of the *y*-axis in each graph is identical to provide information on the sensitivity of the model.



30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
a
Last Year's Bobwhite Count
Predicted Bobwhite Count
30
25
20
15
10
5
0
-4
-3
-2
-1
0
1
2
3
4
b
Deviation from Long-term Mean June Temperature
30
25
20
15
10
5
0
0
0.25
0.5
0.75
1
1.25
1.5
c
Livestock Density (head/ha) on Noncultivated Land

which point, the model predicted that current abundance would near 14 bobwhites. Between previous year's counts of 15 through 30, the predicted bobwhite count was approached a maximum predicted count of 16 bobwhites. Previous year's counts >30 bobwhites resulted in a slight decline in predicted bobwhite abundance. It appeared that the decline was accelerating, but at 65 bobwhites counted in the previous year, the predicted count had declined only by approximately 1 bobwhite from the high of 16.

Predicted bobwhite counts were a decreasing function of the deviation from long-term mean June temperature (Fig. 6.2). Predicted bobwhite counts increased with cooler than normal conditions. When mean June temperature was 3 degrees cooler than normal, predicted bobwhite abundance was highest at approximately 26 bobwhites. Predicted bobwhite counts declined as mean June temperature approached the long-term mean in a slightly decelerating fashion. When mean June temperature was at its long-term mean, predicted abundance was approximately 11 bobwhites. As mean June temperature increased over normal, bobwhite counts steadily declined to a low of 5 at 3 degrees above the long-term mean.

Predicted bobwhite abundance was also a decreasing function of the density of livestock on uncultivated lands (Fig. 6.2). This relationship was also slightly decelerating over the range of observed values. Bobwhite abundance was predicted to be highest when livestock density was <0.25 head/ha. At 0.25 head/ha, abundance is predicted to be approximately 16 bobwhites. At higher livestock densities, bobwhite abundance steadily declines. At >1 head/ha, abundance is at approximately 5 bobwhites.

Discussion

Bobwhite populations in Texas, like those in Oklahoma (Chapter 4), appear to be more sensitive to the magnitude of deviations from normal conditions than to actual weather patterns. The climate model contained only a single climate variable: deviation from long-term mean June temperature. Similarly, only July temperature and fall precipitation were highly relevant in the weather model (Chapter 5, Table 5.2), with other weather variables contributing <10% to the weather model's predictions. Livestock density and previous year's counts were highly relevant in the weather and climate models (Table 5.2).

The variable that contributed the most to climate model predictions was previous year's bobwhite count (Fig. 6.2). The results indicated that density dependent processes influence bobwhite population dynamics. Predicted abundance increased when previous year's count was <15 bobwhites. At previous year's counts >30 bobwhites, predicted bobwhite abundance began to decline, albeit slowly (Fig. 6.2). The weather model predicted a similar but weaker pattern of density dependence (Fig. 5.4c). Roseberry and Klimstra (1984) believed that bobwhite harvest maintained populations at densities below those at which density dependence reduced production. Our results suggest that at low densities, population density had a positive effect on production. At intermediate and high densities, negative effects begin to manifest and production and/or survival begins to reduce abundance.

Deviation from long-term mean June temperature was the second largest contributor to climate model predictions. However, deviation from normal June temperature had a higher relative effect on bobwhite abundance than previous year's count or livestock abundance (Fig. 6.2). At June temperatures below the long-term mean, predicted abundance can be as much as 2.5× the abundance when June temperature is normal. Over the entire 6˚C range of temperature deviations, abundance varied nearly 7 fold. Below average June temperatures also had a greater impact on abundance than did hotter than average temperatures.

As stated in Chapter 4, the data suggest that bobwhites have adapted to the local climate conditions. However, it is also clear that bobwhites might occupy an area where conditions are near the upper limits of their thermal tolerance, because abundance rapidly increased as June temperature became cooler than normal. If the climate in Texas was more amenable to bobwhites, one would expect that cooler temperatures would have a weak positive or negative effect, or a neutral effect.

The final variable in the model was livestock density (head/ha) on noncultivated land. Both the weather (Chapter 5) and the climate model predicted that bobwhite abundance should decline with increasing livestock density. However, the decline predicted by the climate model was more gradual than that from the weather model. Bobwhite abundance increased dramatically below nominal livestock densities according to the weather model predictions (Fig. 5.4). The climate model predicted a nearly linear decline in abundance with increasing livestock density (Fig. 6.2).

Although grazing does not usually lead to a total transformation of the vegetation community, grazing can influence both the structure and species composition of the landscape (Fleischner 1994). The magnitude of the effects depends on the intensity and periodicity of the grazing. Further, whether the structural and compositional changes negatively or positively affect habitat suitability will depend on the magnitude of the changes (Severson and Urness 1994). My results support the idea that increasing the intensity of grazing, as indexed by livestock density, results in greater habitat alteration to the detriment of bobwhite production and survival. Although the optimal habitat configuration and composition for bobwhites varies across their range (Guthery 1999), structural components necessary for successful production and survival may decline with increasing grazing pressure (Archer and Smeins 1991, Fleischner 1994). Further, the amount and effectiveness of vegetation as thermal cover might be reduced by grazing (Barnes et al. 1991). The effect of grazing, therefore, could intensify the effects of June temperature on abundance, particularly when June temperature is higher than normal (Fig 6.2).

Although the climate model better accounted for the variation in bobwhite counts, weather events, particularly weather catastrophes, undoubtedly impact abundance (Errington 1936, 1939, 1941; Roseberry 1962, 1964). However, weather conditions, by virtue of the presence of bobwhite populations, must be at least tolerable for them. In fact, climate is one of the major factors limiting the geographic distribution of species (Gaston 2003:27). Within their geographic range boundaries, species can acclimate to local climate conditions (Gaston

2003:36). It is not surprising, therefore, that bobwhite populations responded more strongly to deviations from the conditions to which they have adapted.

CHAPTER 7

POTENTIAL EFFECTS OF GLOBAL CLIMATE CHANGE ON NORTHERN BOBWHITE ABUNDANCE[1]

Abstract

Predicted changes in global and regional climate are expected to impact the distribution and abundance of wildlife species. The northern bobwhite is no exception. Given the importance of the bobwhite to local and state economies, understanding how climate change might impact the species is important. Further, changes in the distribution of bobwhites could render management policies ineffectual if climate pushes bobwhites out of areas where management is currently focused. I used neural network models to examine the impacts of changes in temperature and precipitation under 2 climate change scenarios: the Goddard Institute for Space Studies (GISS) and the Oregon State University (OSU) general circulation models. These models predict monthly temperature and precipitation under varying assumptions given a two-fold increase in atmospheric concentrations of CO_2. Predictions were available at a 0.5×0.5° latitude–longitude grid for Oklahoma and Texas. I used these predictions as inputs and used the trained neural network weather models developed in Chapters 4 and 5. For Texas, in addition to the climate change predictions, I also used the long-term mean weather conditions as inputs in the model. I estimated the deviation of bobwhite abundance predicted from the climate change data from abundance predicted from the long-term mean weather data. The neural models predicted only declines in bobwhite abundance in Texas and Oklahoma. In some parts of Texas, declines could reach >30 bobwhites per route.

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[1] This chapter has not been previously published.

Introduction

Global change encompasses changes in land cover and land use, and changes in climate and weather patterns (Walker and Steffan 1999). Although land use and cover changes might be the more immediate threat to species and the ecosystems they inhabit and maintain (Walker and Steffan 1999), climate change, because of its global scope and long-term, persistent effects, will have a greater overall impact. Current-generation general circulation models (GCM) predict increases in the global mean temperature of between 1.4 and 5.8 °C by the year 2100 over 1990 mean temperature. Although these predictions are controversial, the National Research Council of the National Academy of Science (NRC 2000: 2) stated, "[i]n the opinion of the panel, the warming trend in global-mean surface temperature observations during the past 20 years is undoubtedly real and is substantially greater than the average rate of warming during the twentieth century." The Intergovernmental Panel on Climate Change concurred (IPCC 2001). Therefore, there is consensus among the scientific community regarding the validity of climate change.

Global climate change is thought to be driven by increases in carbon dioxide (CO_2) and other greenhouse gas concentrations in the atmosphere (Schneider 1993, Bryant 1997, IPCC 2001). The concentration of CO_2 has increased in the Earth's atmosphere by 31% since the 1750s and is higher than at any other point in the last 400,000 years (IPCC 2001), and concentrations of other greenhouse gases have also increased at unprecedented rates in recent history (Walker and Steffan 1999, IPCC 2001). Normal fluctuations in CO_2 concentrations have ranged between 190 ppmv (parts per million by volume) to 280 ppmv, but have only increased to the high end of this range since the advent of the Industrial Revolution (NRC 2001). The role of these greenhouse gases in climate change results from their absorption of long-wave radiation emitted from the earth's surface (Bryant 1997), thereby reducing the amount of heat energy that is radiated into space. This is called the greenhouse effect and results in increased surface temperature.

Models of climate change, called general circulation models (GCMs), are collections of simultaneous, nonlinear equations based on some basic laws of physics, which describe the behavior of the atmosphere and oceans as influenced by the earth's rotation and temperature gradients between polar and equatorial regions (Schneider 1993, Bryant 1997). Current generations of GCMs incorporate factors for other variables that can affect climate (Gates 1993). The differences between various models, therefore, are the differences in which of these other factors are taken into account. The GCMs, as applied in climate-change research, are based on the assumption that concentrations of greenhouse gases, particularly CO_2, will double over the historic mean levels within the next century (Schneider et al. 1992, Schneider 1993, IPCC 2001). The GCMs give a picture of the potential future climate, assuming that CO_2 and other greenhouse gas concentrations have stabilized and that the new climate is at an equilibrium state (i.e., the climate is no longer in the process of changing, but has reached its new steady state). Given human reluctance to curb CO_2 emissions, it is possible that the GCM predictions will on the low side of the range of possible oucomes. Although the GCMs perform relatively well at predicting current climate, their performance depends on the controlling factors included in the model and, as a result, there often are discrepancies between model predictions and climate observations (NRC 2000). These discrepancies are undoubtedly the result of the complex nature of the global climate system in addition to the different underlying assumptions (Schneider et al. 1992). However, discrepancies limit the ability to accurately model species responses. If the magnitude of the discrepancies is small, the predictions are likely to be accurate. This is why it is important to understand how species respond to weather and climate, as has been attempted here. Such understanding can be applied to each new generation of GCMs to provide increasingly accurate estimates of the effects of climate change on bobwhites.

Regional and local changes in temperature and precipitation are expected to vary substantially across the globe (Watson et al. 1998). There is a >90% chance that continental interior regions of North America will experience temperature increases greater than the global mean by as much as 40% (IPCC 2001). Further, the diurnal temperature differential will decrease (Easterling et al. 1997). Over the past century, the global mean temperature has already increased by 0.6 °C, with the greatest periods of warming occurring between the periods 1910-1945 and 1976-2000 (IPCC 2001). Because of the increase in the global mean temperature, the extent of snow cover has decreased by 10% since the 1960s and the thickness of the arctic sea ice has declined by 40% since the 1950s (IPCC 2001). Concurrent with the increases in the temperature, global mean rainfall and evaporation are predicted to increase in proportion to the temperature increase (Schneider 1993). Again, the magnitude and seasonality of the increases will vary regionally (Watson et al. 1998). Over the mid-latitudes during the past century, annual rainfall has increased by 0.5 to 1.0%/decade (IPCC 2001). In the sub-tropic areas of the northern hemisphere, rainfall has decreased by 0.3%/decade. Further, the frequency of heavy rainfall has increased by 2-4% over the last century (IPCC 2001), indicating an increase in the number and frequency of catastrophic storms.

My objective was to determine the potential consequences of global climate change for bobwhite distribution and abundance in Texas and Oklahoma, based on the current best-estimate of regional changes in temperature and precipitation. I used a neural network modeling approach and climate change predictions from 2 GCMs: the Goddard Institute for Space Studies model (GISS) and the Oregon State University model (OSU). I predicted abundance (Texas) and standard normal deviate of abundance (Oklahoma) as dependent variables and mean monthly values for June, July, August mean maximum temperature and spring, summer, and fall mean total precipitation from the GCMs. The resulting output can be used by wildlife managers to improve their management plans by taking into account possible changes in distribution and abundance of bobwhites that could result from climate change.

Methods

To predict potential bobwhite abundance and distribution under global climate change scenarios, I used neural network models. The models were developed to predict bobwhite abundance as a function of various weather variables and land-use patterns. A complete description of the models and how they were developed appears in Chapters 4 (Oklahoma) and 5 (Texas). Briefly, the Oklahoma neural model predicted the standard normal deviate of bobwhite counts based on mean maximum June, July, and August temperature (°C); mean total winter (Dec—Feb), spring (Mar—May), and summer (Jun—Aug) precipitation (mm); and proportion of county area in cultivation, livestock density on noncultivated land (head/ha), and the standard normal deviate of last year's bobwhite count. The Texas model predicted bobwhite abundance (bobwhites/route/ecoregion/year) with the same suite of predictor variables, except for the addition of fall (Sep—Nov) precipitation and the substitution of previous year's bobwhite count for the standard normal deviate of the previous year's count.

I used climate change scenarios produced by the VEMAP Phase I database project (Kittel et al. 1996). The database contained climate change scenarios from 8 different GCMs, all of which were based on a doubling of atmospheric CO_2. I selected 2 models for use based on the climate variables predicted by the GCMs. Using 2 models also provides information on how the underlying assumptions of the various GCMs might influence the inferences drawn regarding changes in bobwhite abundance. The 2 models selected were the Goddard Institute for Space Studies (GISS; Hansen et al. 1988) model and the Oregon State University (OSU; Schlesinger and Zhao 1989) model. The VEMAP (Vegetation/Ecosystem Modeling and Analysis Project) used the existing models to produce datasets of long-term mean climate, soils, vegetation, and climate change scenarios for the conterminous United States (Kittel et al. 1996). These datasets contain mean monthly climate variables (precipitation and temperature) at a 0.5 ° latitude–longitude scale.

I extracted data for temperature and precipitation for Texas and Oklahoma. However, the data points were not in a usable form when extracted from the database. Temperature data were represented as temperature at 2×CO_2 minus temperature at 1×CO_2. Precipitation data were represented as the ratio between rainfall at 2×CO_2 and 1×CO_2 concentrations. To obtain usable data, I also extracted base climate conditions (1×CO_2) gridded to the same 0.5 ° latitude/longitude scale as the climate change scenarios. Using these base-condition data, I was able to calculate monthly values for mean maximum monthly temperature and mean total monthly rainfall under 2×CO_2 concentrations. After obtaining usable data, I extracted June, July, and August mean maximum temperatures, and estimated mean total winter, spring, summer, and fall precipitation for use as inputs into the trained neural models. I used the mean values for the proportion of county area in cultivation, the density of livestock on noncultivated land, and the previous year's bobwhite count (or, in the case of Oklahoma, the mean standard normal deviate of the bobwhite counts), because there were no models available to predict changes in these values by 2100.

Climate change scenarios were presented to the trained neural networks to obtain predicted bobwhite abundance (Texas) or the standard normal deviate of bobwhite abundance (Oklahoma). As discussed above, the Oklahoma model predicted the deviation of the bobwhite count from the long-term mean (represented as the standard normal deviate). The output from the Oklahoma model was imported into ArcView 3.3 (ESRI, Redmond, California, USA). I used the Kriging Interpolator (Nieuwland Automatisering, Amsterdam, Netherlands) and the Spatial Analyst (ESRI, Redmond, California, USA) extensions to interpolate the point output onto a surface, where the surface represents the standard normal deviate of bobwhite abundance under a 2×CO_2 climate change scenario.

A similar process was employed for the Texas predictions, with the addition of a few steps. To obtain deviations from normal bobwhite counts in Texas, I also presented the base weather data (plus the means of the land-use and population variables) to the trained neural model. I then estimated the difference between predicted abundance under 1×CO_2 and 2×CO_2 scenarios. These differences were then imported into ArcView 3.3 and an interpolated surface was generated as for Oklahoma.

To assist with interpreting the graphical output, I also imported the original climate change variables (temperature deviation from 1×CO_2 and precipitation change ratio) into ArcView and interpolated surfaces across Texas and Oklahoma. Precipitation change ratios were averaged over the 3-month seasonal intervals to obtain a seasonal estimate of precipitation change and to facilitate comparison with neural model predictions of bobwhite abundance. Because the results from both GISS and OSU models were qualitatively similar, I focused on the results from the GISS model.

Results and Discussion

The neural network models for Texas and Oklahoma predicted declines when presented with climate change data from the GISS (Fig. 7.1 and 7.2) and OSU GCMs. The magnitude of the declines varied across states. In Texas, the declines were predicted to be greatest in the southern part of the state (South Texas Plains; Fig. 7.1). Reductions were predicted to be lower in the Panhandle and northern Texas. Predicted climate changes reduced bobwhite abundance across the state (Fig. 7.1). That is, there were no areas of Texas for which bobwhite abundance was predicted to improve or stay at current levels. In southern portions of Texas, the declines are predicted to be quite significant (Fig. 7.1), with some areas suffering >20 bobwhites/route reductions.

Reductions in bobwhite abundance were also the norm in Oklahoma, where the predicted standard normal deviate of bobwhite abundance was negative across the state (Fig. 7.2). The pattern of decline varied from that predicted by the Texas model, however. Declines were predicted to be greatest in north central and western parts of Oklahoma and lowest in southeastern Oklahoma (Fig. 7.2). This latter area of the state includes portions of the Ouachita National Forest, where bobwhite abundances are low because forest habitat is not preferred by bobwhites (Cram et al. 2002). The neural model, however, is spatially naïve. That is, it makes it predictions only on the information provided to it. As a result, it cannot take into account factors, such as forest cover, that might limit bobwhite abundance independent of the

Fig. 7.1. Predicted changes in northern bobwhite abundance in Texas based on climate change scenarios developed from the Goddard Institute of Space Science general circulation model (GISS GCM). Predictions were based on a 0.5×0.5° latitude/longitude grid and interpolated over the entire state using universal kriging.

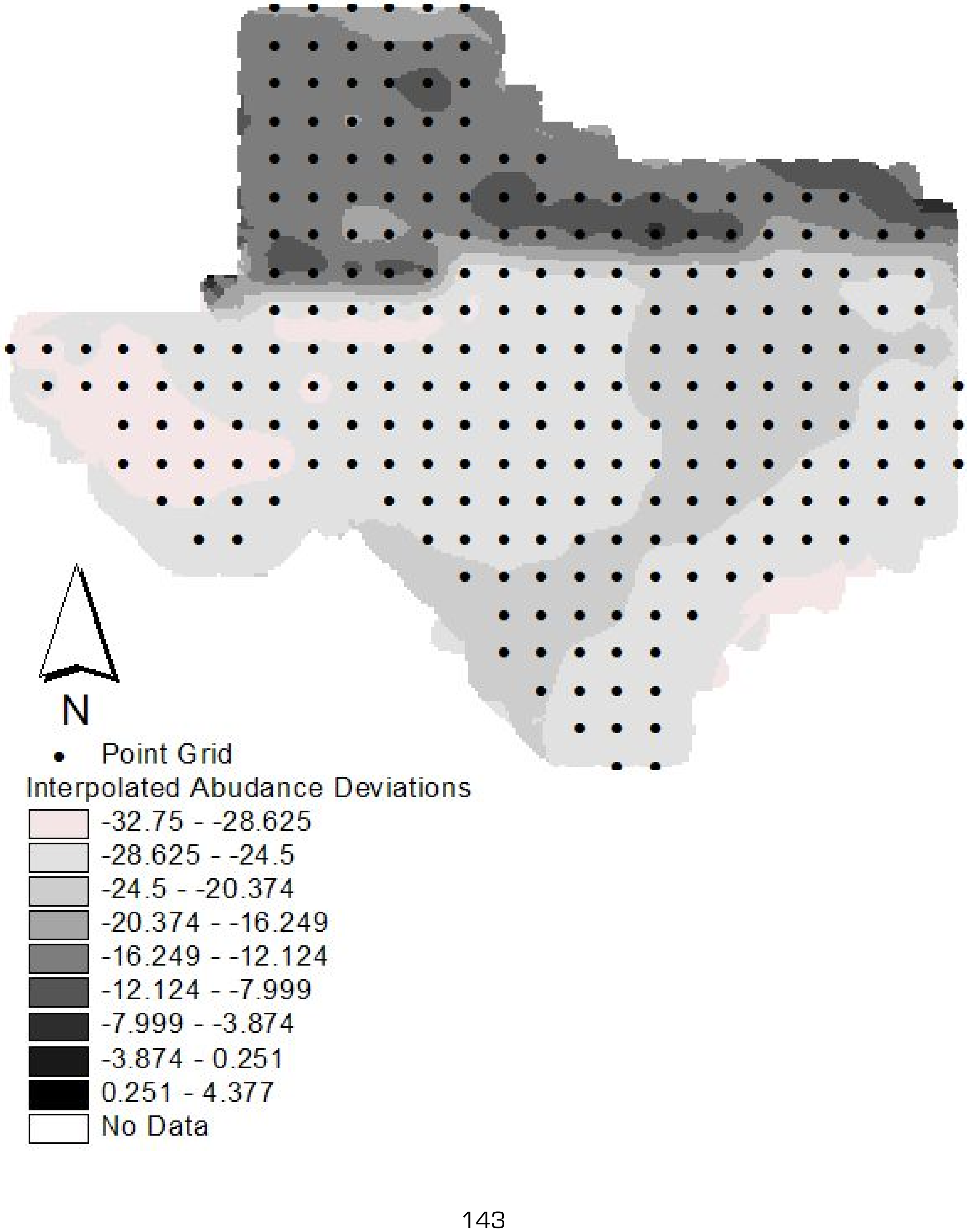
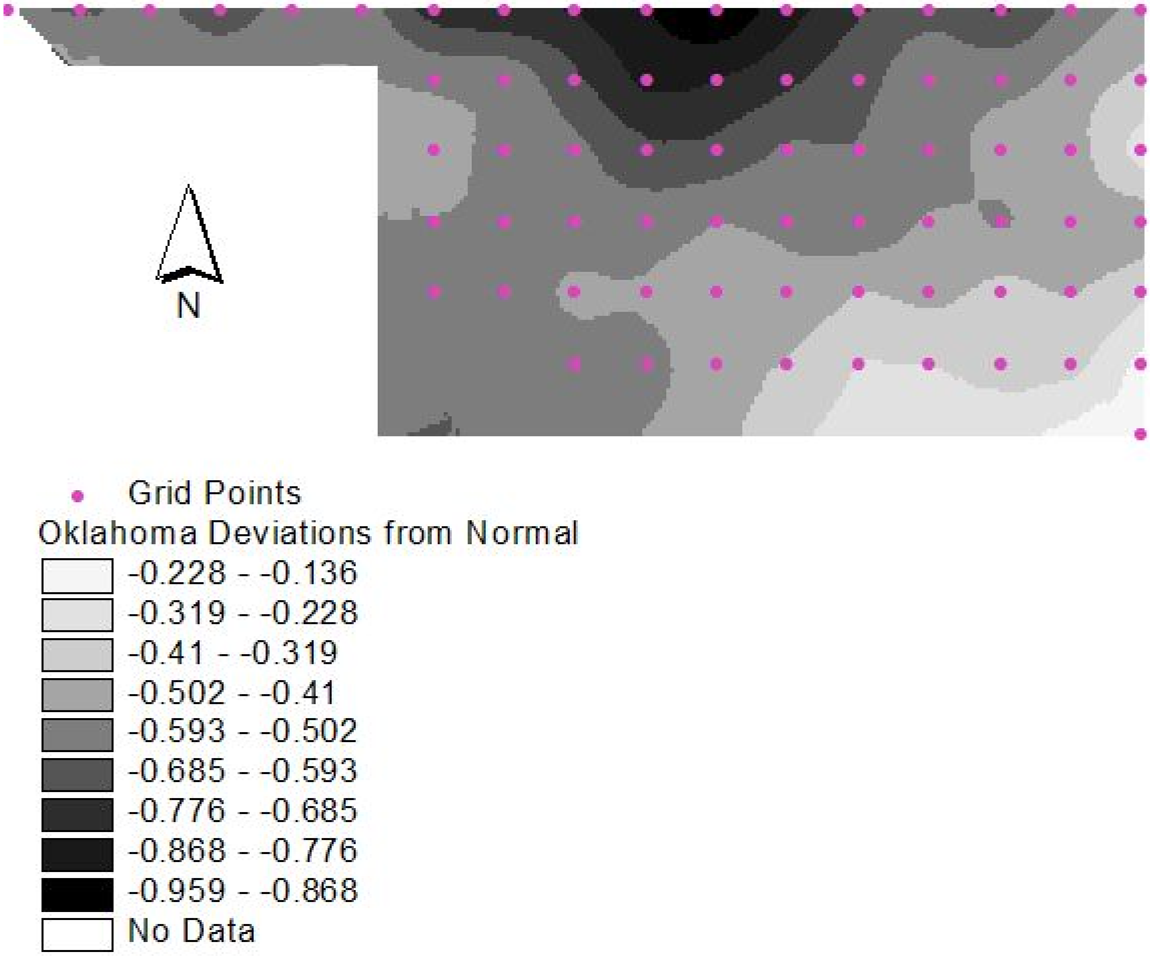

N
Point Grid
Interpolated Abudance Deviations
-32.75 - -28.625
-28.625 - -24.5
-24.5 - -20.374
-20.374 - -16.249
-16.249 - -12.124
-12.124 - -7.999
-7.999 - -3.874
-3.874 - 0.251
0.251 - 4.377
No Data

Fig. 7.2. Predicted changes in standard normal deviate of bobwhite counts in Oklahoma based on climate change scenarios developed from the Goddard Institute of Space Science general circulation model. The predictions were based on a 0.5×0.5° latitude/longitude grid and interpolated across the state using universal kriging.


N
Grid Points
Oklahoma Deviations from Normal
-0.228 - -0.136
-0.319 - -0.228
-0.41 - -0.319
-0.502 - -0.41
-0.593 - -0.502
-0.685 - -0.593
-0.776 - -0.685
-0.868 - -0.776
-0.959 - -0.868
No Data

factors included in the model. The prediction, therefore, that bobwhite declines would be lowest in the southeast implicitly assumes that suitable habitat is available for bobwhites.

The interpolated contours for June, July, and August temperature under $2\times CO_2$ concentrations showed the month-to- month variation in the magnitude and spatial distribution of temperature increases in Oklahoma (Figs. 7.3—7.5). These figures show the predicted change (°C) in temperature from baseline GCM ($1\times CO_2$ concentrations) predictions for Oklahoma. June temperature is predicted to increase between 3.2 and 3.7 °C, with the greatest increases in the southeastern portion of the state. This is the region where deviations in bobwhite abundance were lowest under the climate change scenario (Fig. 7.2). July and August temperature increases were highest in the western portions of Oklahoma (Figs. 7.4 and 7.5); again, areas where bobwhite declines are only moderately high under the climate change scenario.

Patterns of change in seasonal precipitation regimes are equally as varied, both in magnitude and in spatial distribution in Oklahoma (Figs. 7.6—7.9). The change ratios depicted in the figures represent the ratio between rainfall at $2\times CO_2$ atmospheric concentrations and at $1\times CO_2$ concentrations. Values >1.0 indicate rainfall higher than current levels and values <1.0 indicate rainfall below current levels. The GCMs predicted that winter rainfall would be below current levels in western, and higher than current levels in eastern Oklahoma (Fig. 7.6). Spring rainfall was predicted to be below current levels statewide, with the greatest declines in the west (Fig. 7.7). Summer (Fig. 7.8) and fall (Fig. 7.9) rainfall were predicted to increase over current levels, with the greatest increases in the eastern parts of Oklahoma in summer and western parts in fall. The pattern of precipitation change for Oklahoma, therefore, will be for relatively drier conditions in the west and increasingly wetter conditions in the east. Patterns of decline in bobwhite abundance (Fig. 7.2) indicated an east—west gradient, albeit less distinct, with greater decreases in the southwest.

In Texas, all temperature changes were predicted to be positive. June temperature increases were predicted to be greatest in south Texas, although the increases were

Fig. 7.3. Change in June temperature for Oklahoma as predicted by the Goddard Institute for Space Science general circulation model. The values represent the difference between model predictions at 2×CO_2 and 1×CO_2 concentrations.

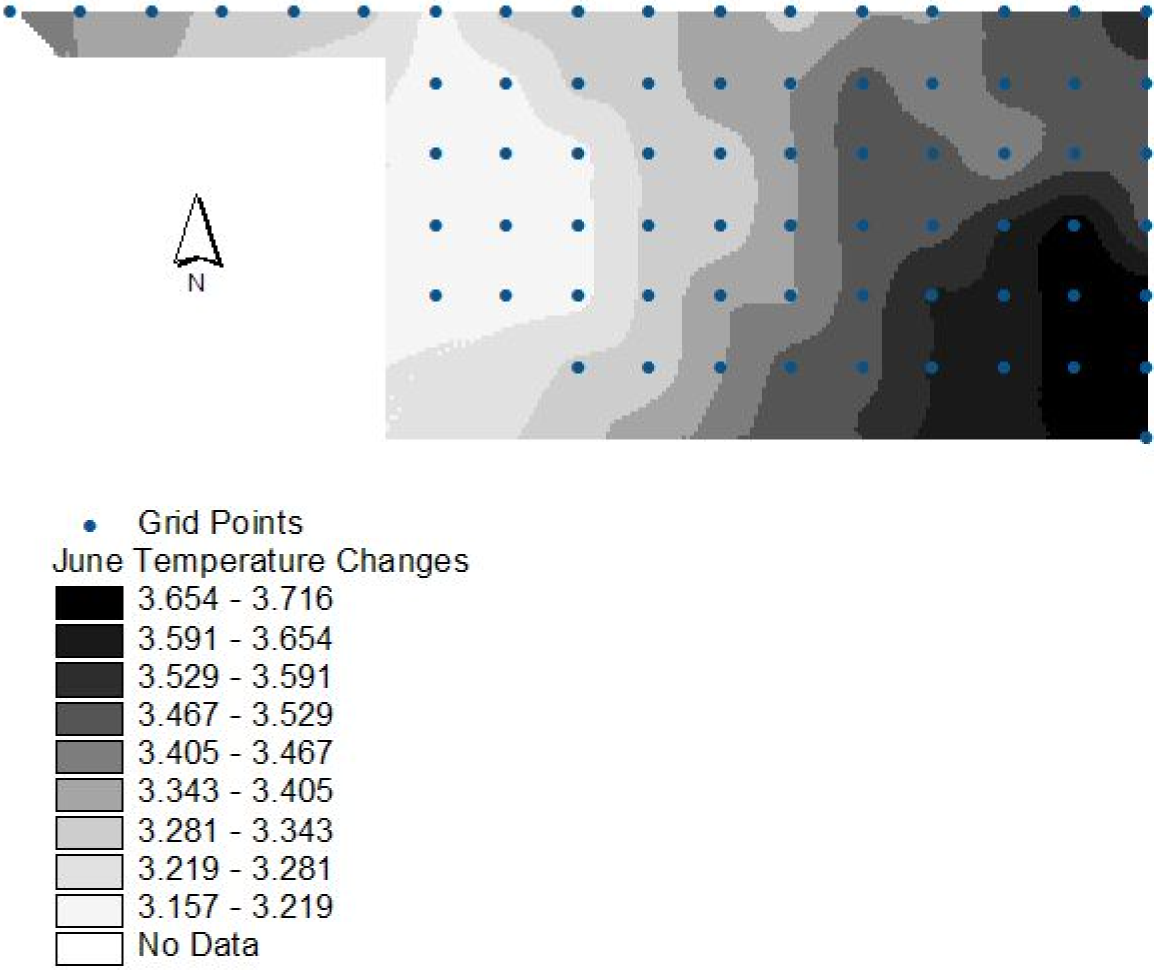

N
Grid Points
June Temperature Changes
3.654 - 3.716
3.591 - 3.654
3.529 - 3.591
3.467 - 3.529
3.405 - 3.467
3.343 - 3.405
3.281 - 3.343
3.219 - 3.281
3.157 - 3.219
No Data

Fig. 7.4. Change in July temperature for Oklahoma as predicted by the Goddard Institute for Space Science general circulation model. The values represent the difference between model predictions at 2×CO_2 and 1×CO_2 concentrations.

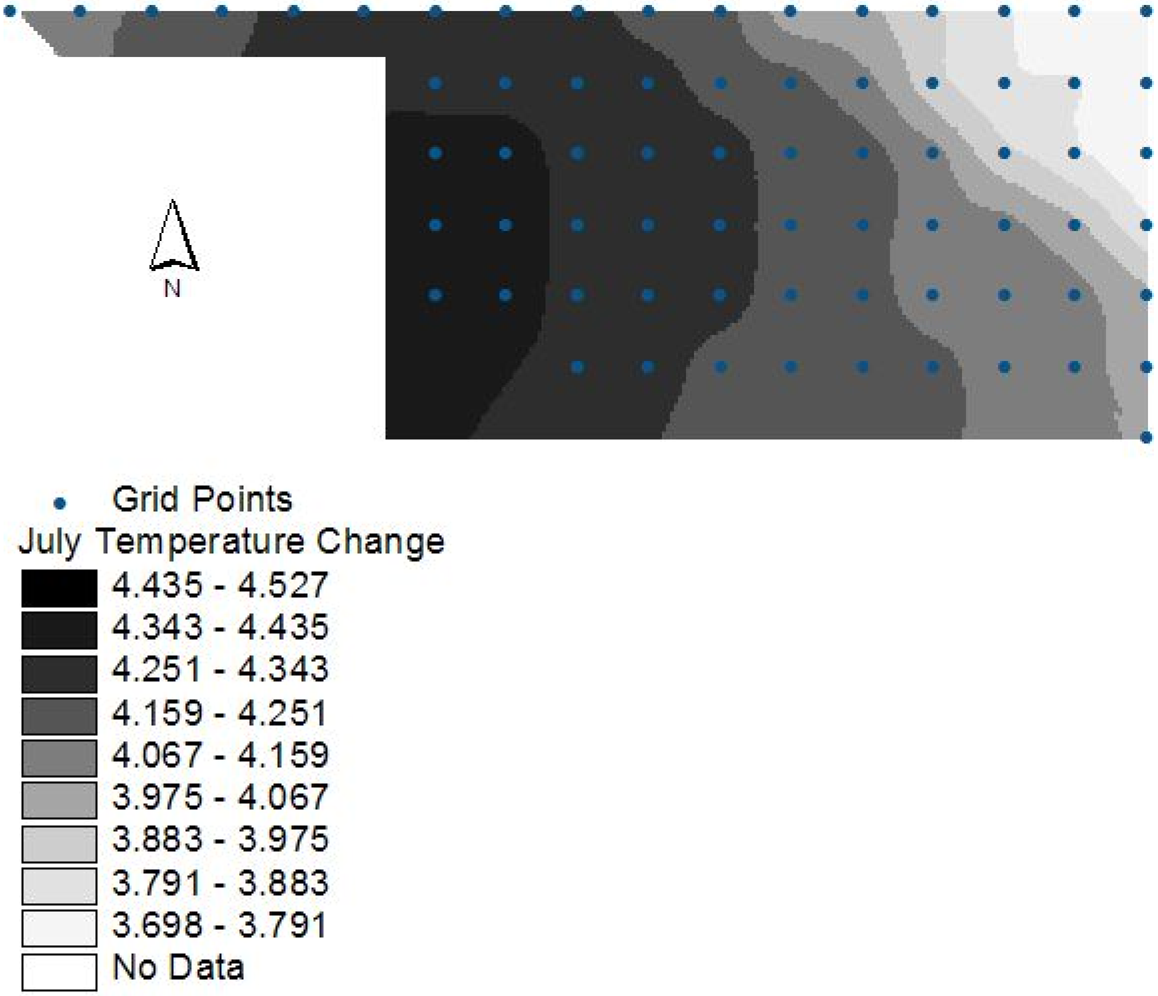

N
Grid Points
July Temperature Change
4.435 - 4.527
4.343 - 4.435
4.251 - 4.343
4.159 - 4.251
4.067 - 4.159
3.975 - 4.067
3.883 - 3.975
3.791 - 3.883
3.698 - 3.791
No Data

Fig. 7.5. Change in August temperature for Oklahoma as predicted by the Goddard Institute for Space Science general circulation model. The values represent the difference between model predictions at $2\times CO_2$ and $1\times CO_2$ concentrations.

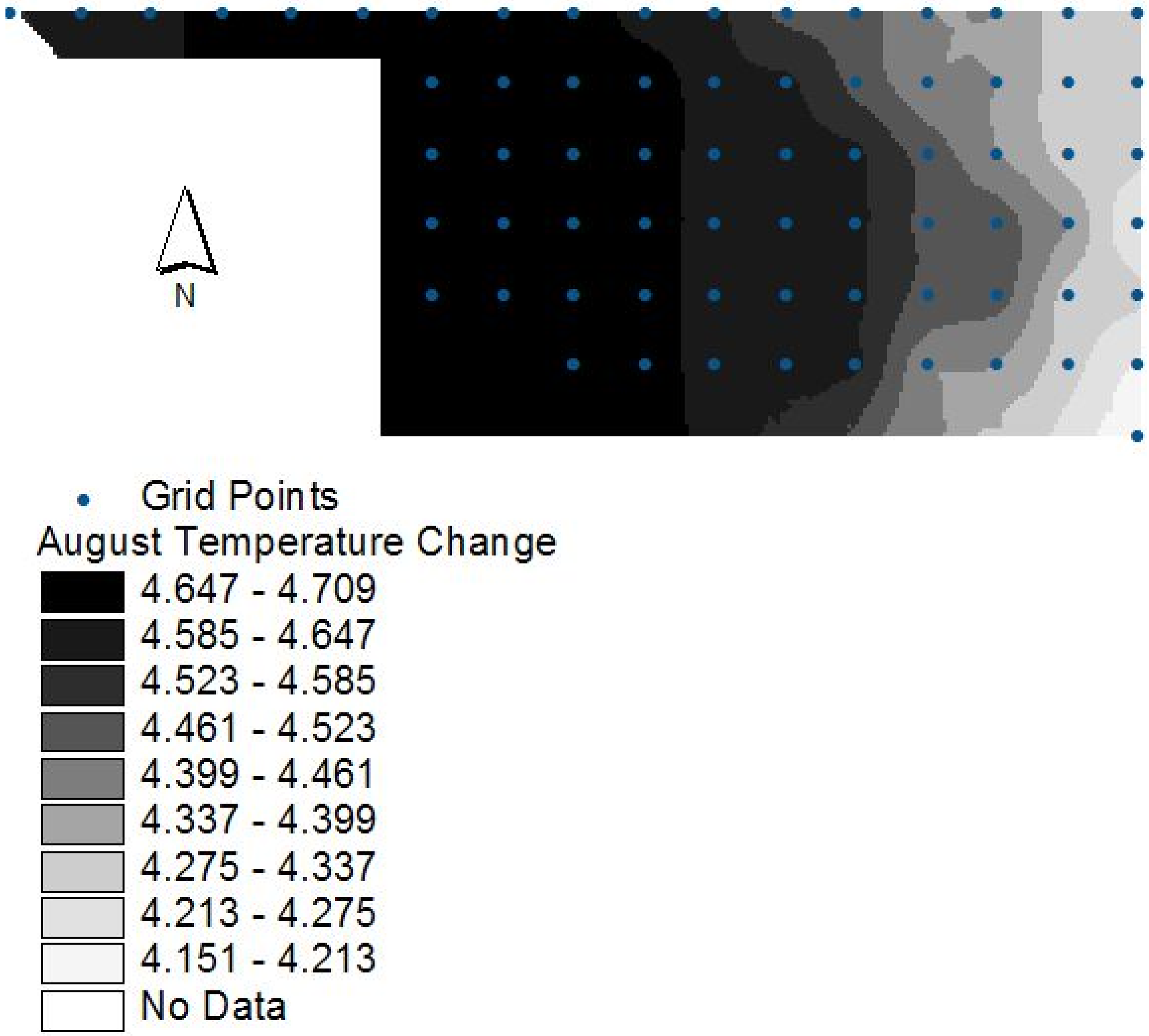

N
Grid Points
August Temperature Change
4.647 - 4.709
4.585 - 4.647
4.523 - 4.585
4.461 - 4.523
4.399 - 4.461
4.337 - 4.399
4.275 - 4.337
4.213 - 4.275
4.151 - 4.213
No Data

Fig. 7.6. Change in winter rainfall for Oklahoma as predicted by the Goddard Institute for Space Science general circulation model. The values represent the ratio of model predictions at 2×CO_2 and 1×CO_2 concentrations.

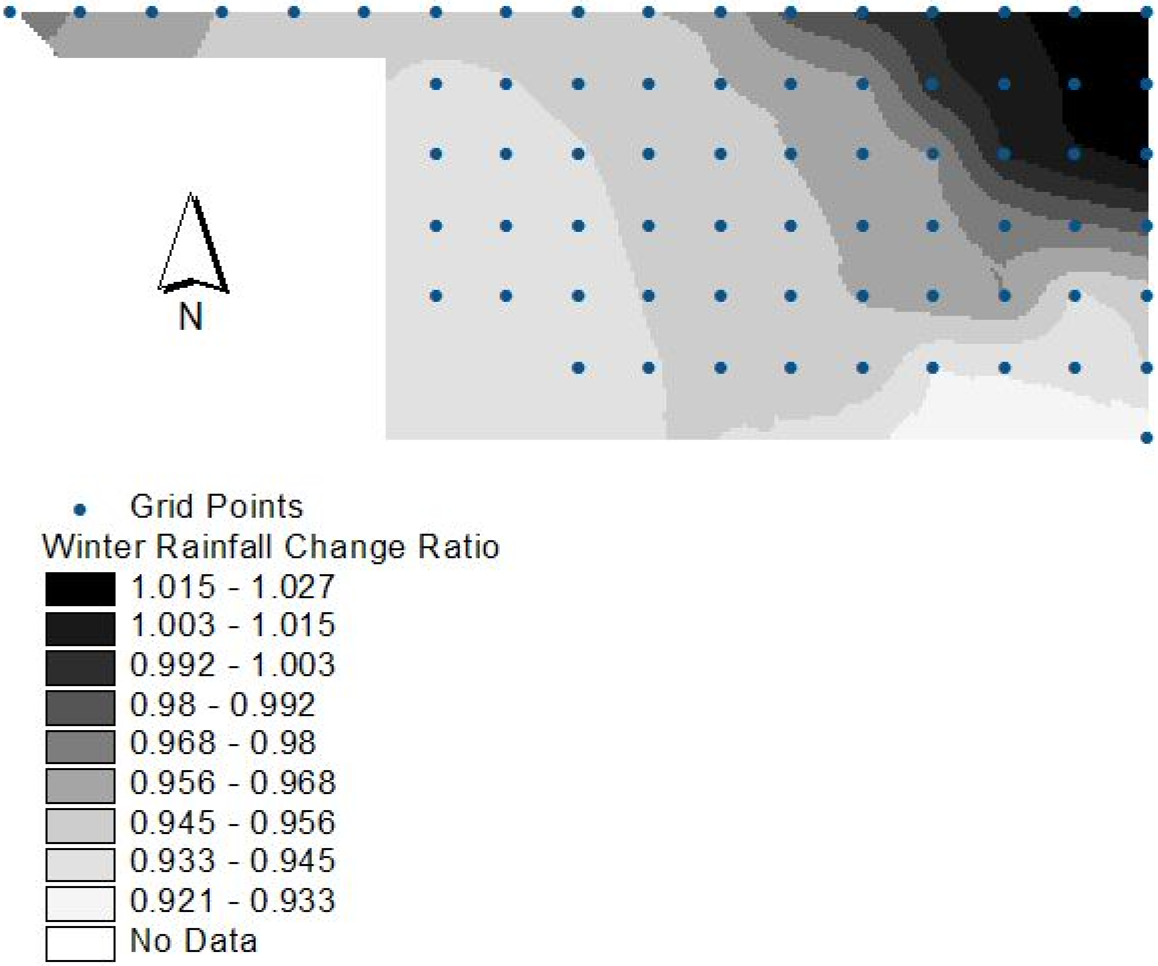

N
Grid Points
Winter Rainfall Change Ratio
1.015 - 1.027
1.003 - 1.015
0.992 - 1.003
0.98 - 0.992
0.968 - 0.98
0.956 - 0.968
0.945 - 0.956
0.933 - 0.945
0.921 - 0.933
No Data

Fig. 7.7. Change in spring rainfall for Oklahoma as predicted by the Goddard Institute for Space Science general circulation model. The values represent the ratio of model predictions at 2×CO_2 and 1×CO_2 concentrations.

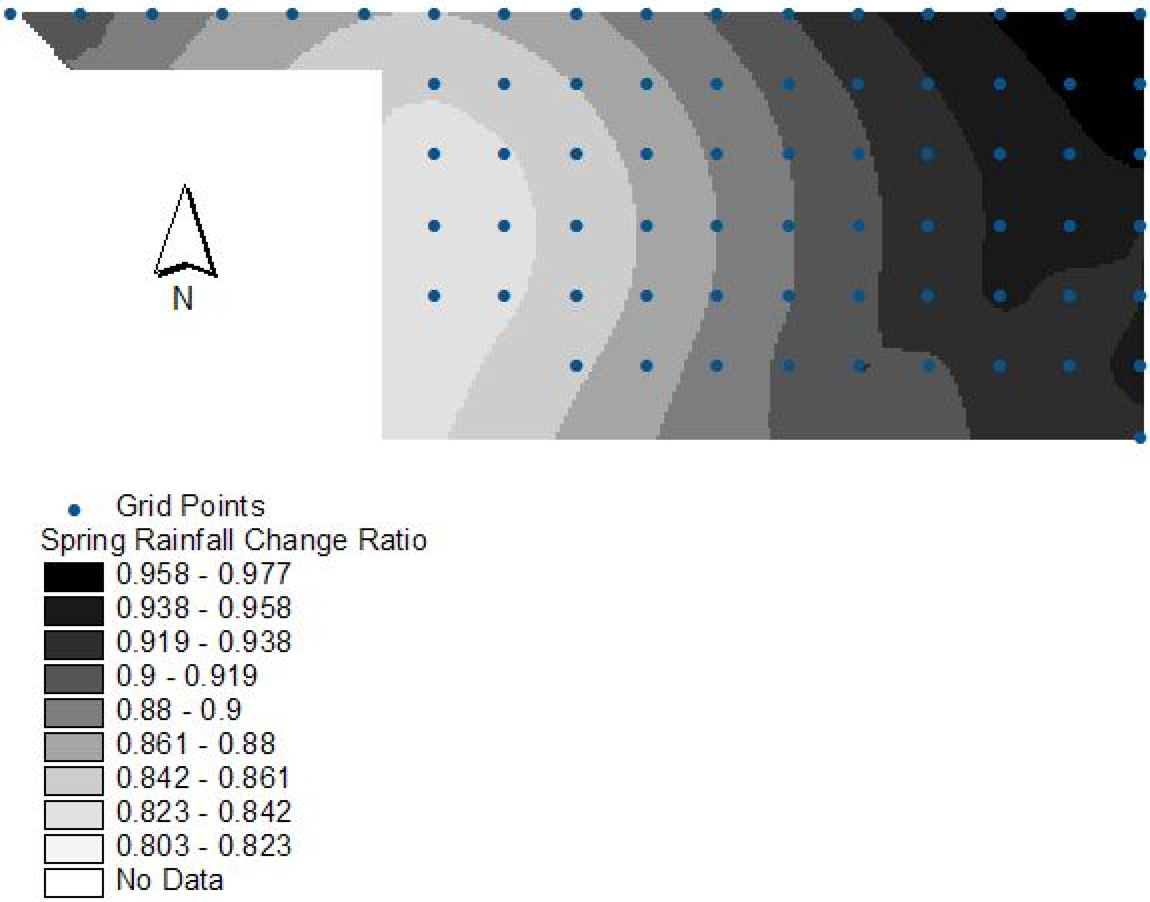

N
Grid Points
Spring Rainfall Change Ratio
0.958 - 0.977
0.938 - 0.958
0.919 - 0.938
0.9 - 0.919
0.88 - 0.9
0.861 - 0.88
0.842 - 0.861
0.823 - 0.842
0.803 - 0.823
No Data

Fig. 7.8. Change in summer rainfall for Oklahoma as predicted by the Goddard Institute for Space Science general circulation model. The values represent the ratio of model predictions at $2\times CO_2$ and $1\times CO_2$ concentrations.

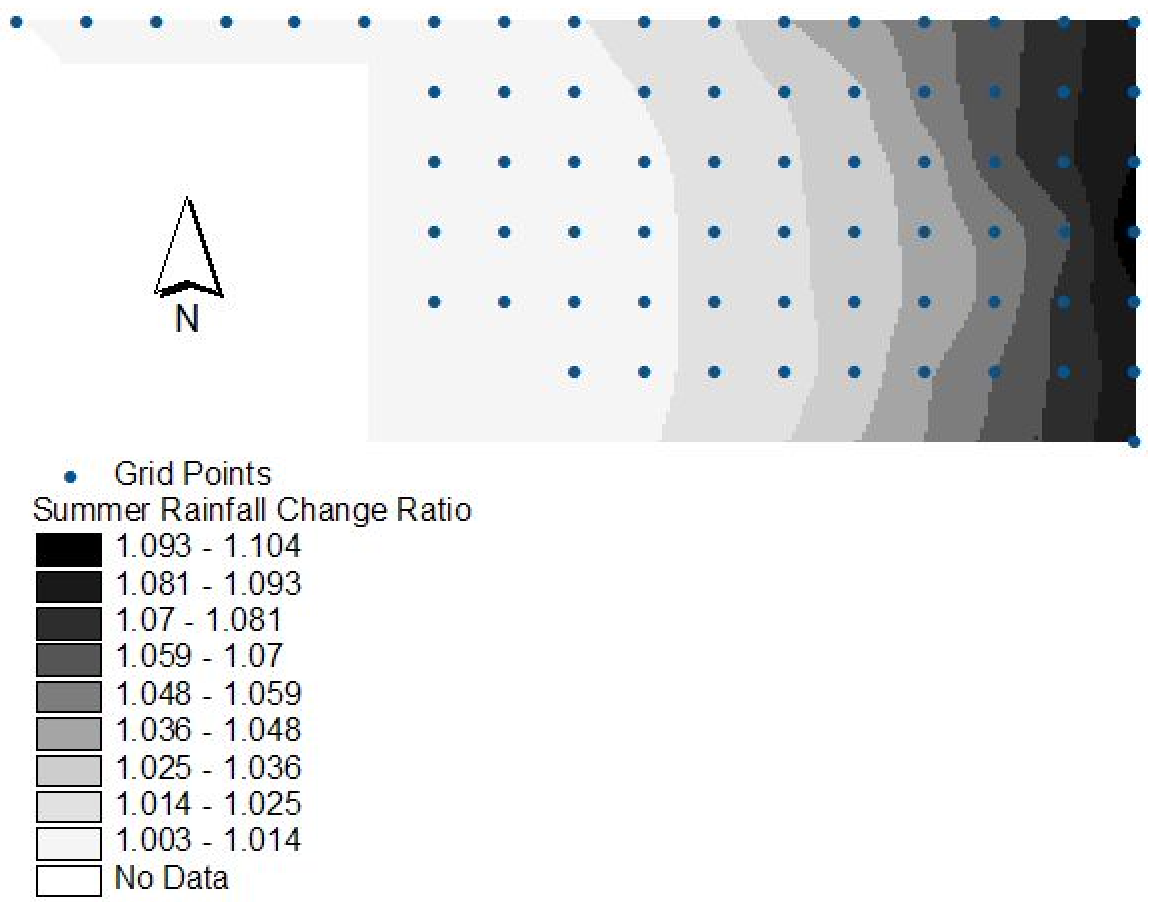
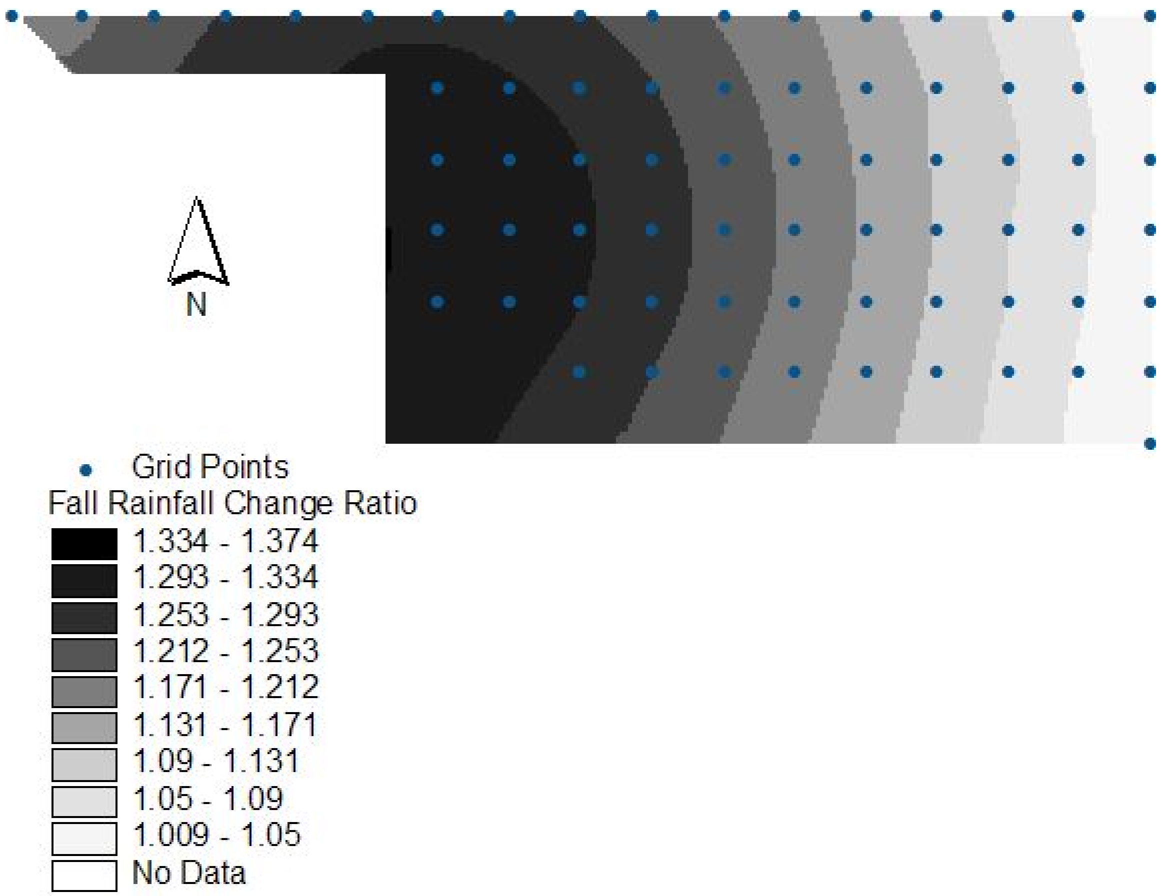

N
Grid Points
Summer Rainfall Change Ratio
1.093 - 1.104
1.081 - 1.093
1.07 - 1.081
1.059 - 1.07
1.048 - 1.059
1.036 - 1.048
1.025 - 1.036
1.014 - 1.025
1.003 - 1.014
No Data

Fig. 7.9. Change in fall rainfall for Oklahoma as predicted by the Goddard Institute for Space Science general circulation model. The values represent the ratio of model predictions at $2\times CO_2$ and $1\times CO_2$ concentrations.


N
Grid Points
Fall Rainfall Change Ratio
1.334 - 1.374
1.293 - 1.334
1.253 - 1.293
1.212 - 1.253
1.171 - 1.212
1.131 - 1.171
1.09 - 1.131
1.05 - 1.09
1.009 - 1.05
No Data

moderate (Fig. 7.10). Temperatures were predicted to increase the least in the northern part of Texas in June, coincident with those areas where bobwhite abundance was predicted to decline the least. Temperature increases in Texas were more dramatic in July (Fig. 7.11) and August (Fig. 7.12), and were greatest in north-central (July) and central (August) Texas.

Like Oklahoma, variation in seasonal precipitation patterns varied spatially in Texas (Figs. 7.13—7.16). Winter precipitation was predicted to be below current levels (Fig. 7.13) over most of the state, except for extreme west Texas. The localized pattern of increased precipitation shifted to the south of Texas in spring (Fig. 7.14), and precipitation in northern Texas was predicted to be well below current levels. Most of central Texas was predicted to be drier than it is currently in summer (Fig. 7.15), but eastern and western portions of Texas were predicted to experience precipitation above current levels (i.e., precipitation at $1\times CO_2$). Comparing changes in August temperature and summer precipitation, note that summer precipitation was predicted to decrease in a large portion of central Texas (Fig. 7.15) where August temperature was predicted to increase the most (Fig. 7.12). This confluence of conditions might produce the high predicted declines in central Texas (Fig. 7.1). Fall precipitation was also predicted to be below current levels in southern and central Texas (Fig. 7.16). Areas where precipitation levels were predicted to be above current levels coincided with areas where bobwhite abundance was predicted to decline the least (Fig. 7.1).

Many of the above-described changes in temperature and precipitation regimes in Texas and Oklahoma were dramatic when compared with current climate conditions. Through what processes these changes will affect bobwhite abundance is a complex question. There are several direct and indirect mechanisms through which global change could bring about the changes listed above. The biotic and abiotic environments are important determinants of species' ecology. Therefore, any change to that environment, by definition, will have some impact on the species involved, especially if changes occur at a rate faster than the species can adapt either genetically. Behavioral adaptations, such as earlier nesting, could help maintain bobwhite populations until genetic adaptation occurs.

Fig. 7.10. Change in June temperature as predicted by the Goddard Institute for Space Science general circulation model for Texas. The values represent the difference between model predictions at 2×CO_2 and 1×CO_2 concentrations.

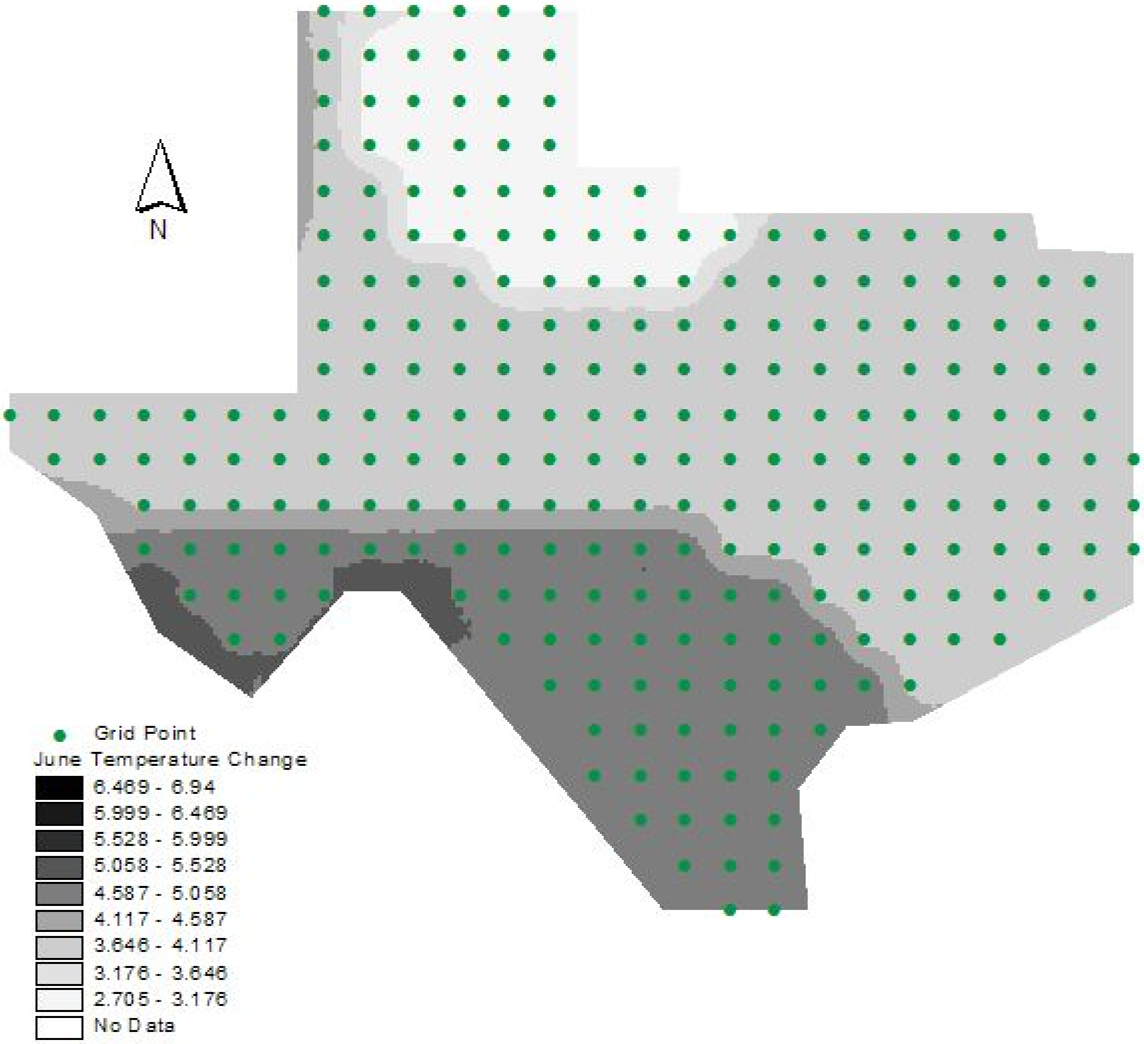

N
Grid Point
June Temperature Change
6.469 - 6.94
5.999 - 6.469
5.528 - 5.999
5.058 - 5.528
4.587 - 5.058
4.117 - 4.587
3.646 - 4.117
3.176 - 3.646
2.705 - 3.176
No Data

Fig. 7.11. Change in July temperature as predicted by the Goddard Institute for Space Science general circulation model for Texas. The values represent the difference between model predictions at $2\times CO_2$ and $1\times CO_2$ concentrations.

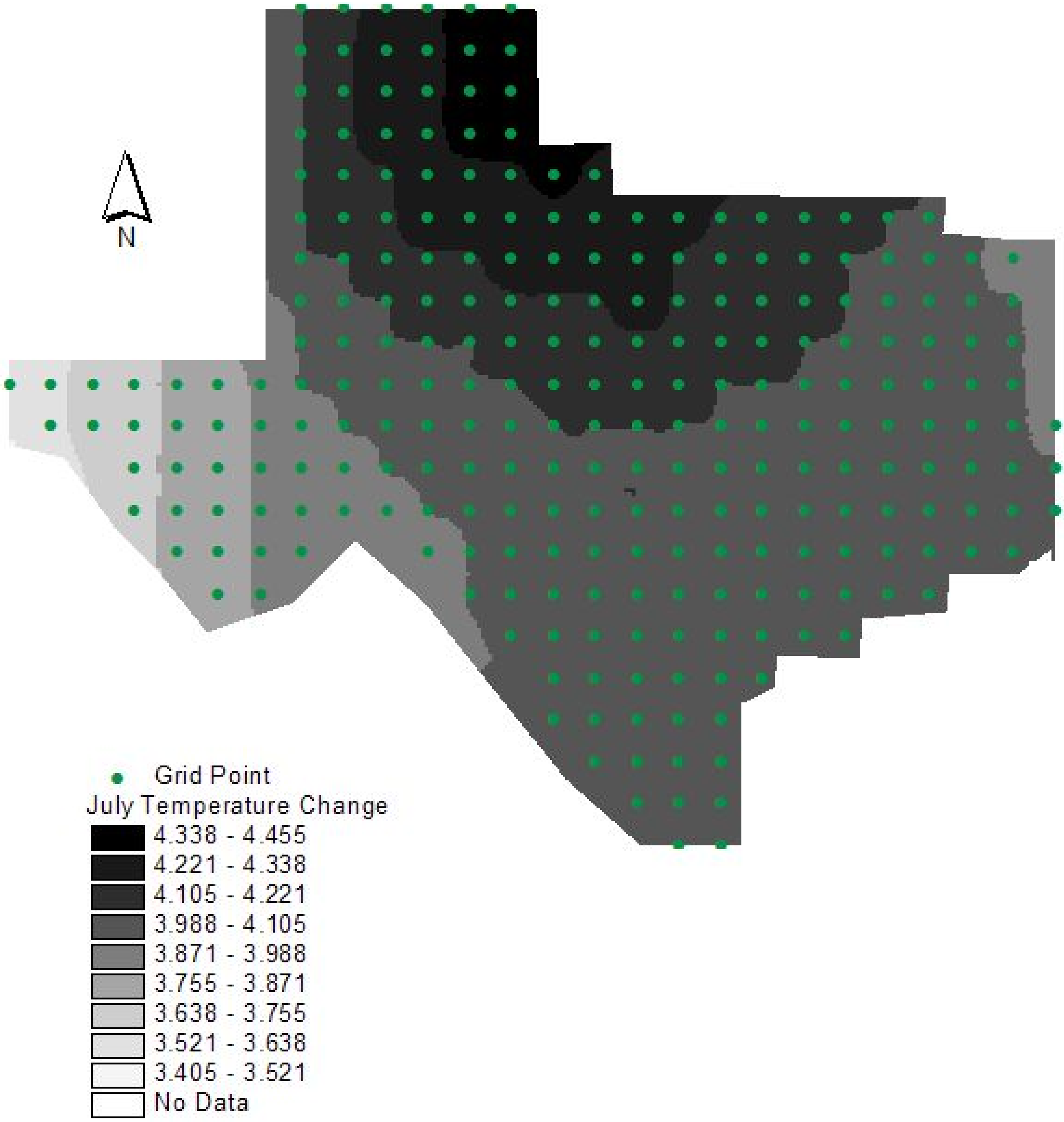

N
Grid Point
July Temperature Change
4.338 - 4.455
4.221 - 4.338
4.105 - 4.221
3.988 - 4.105
3.871 - 3.988
3.755 - 3.871
3.638 - 3.755
3.521 - 3.638
3.405 - 3.521
No Data

Fig. 7.12. Change in August temperature as predicted by the Goddard Institute for Space Science general circulation model for Texas. The values represent the difference between model predictions at 2×CO_2 and 1×CO_2 concentrations.

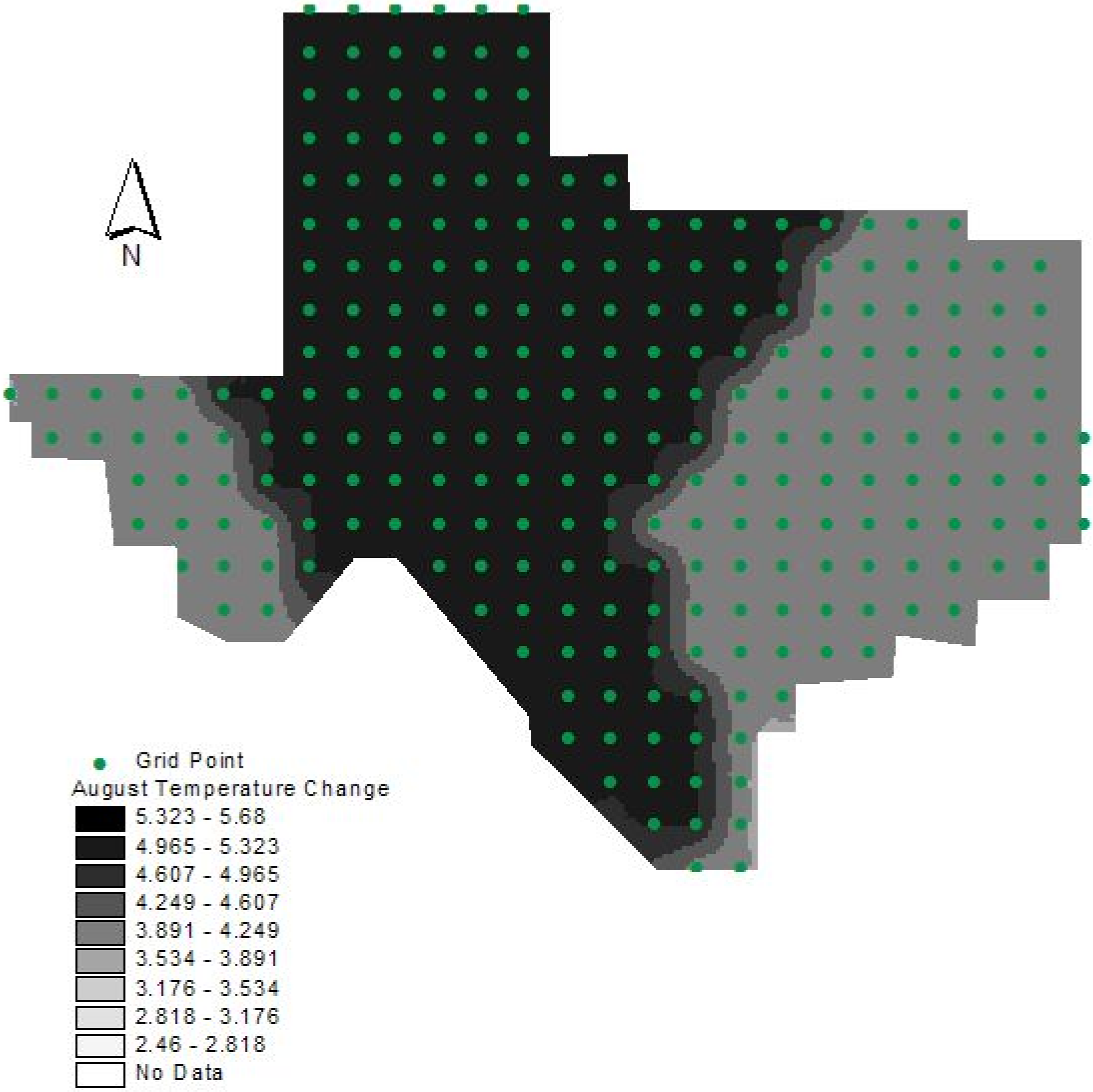

N
Grid Point
August Temperature Change
5.323 - 5.68
4.965 - 5.323
4.607 - 4.965
4.249 - 4.607
3.891 - 4.249
3.534 - 3.891
3.176 - 3.534
2.818 - 3.176
2.46 - 2.818
No Data

Fig. 7.13. Change in winter rainfall as predicted by the Goddard Institute for Space Science general circulation model for Texas. The values represent the ratio of model predictions at $2\times CO_2$ and $1\times CO_2$ concentrations.

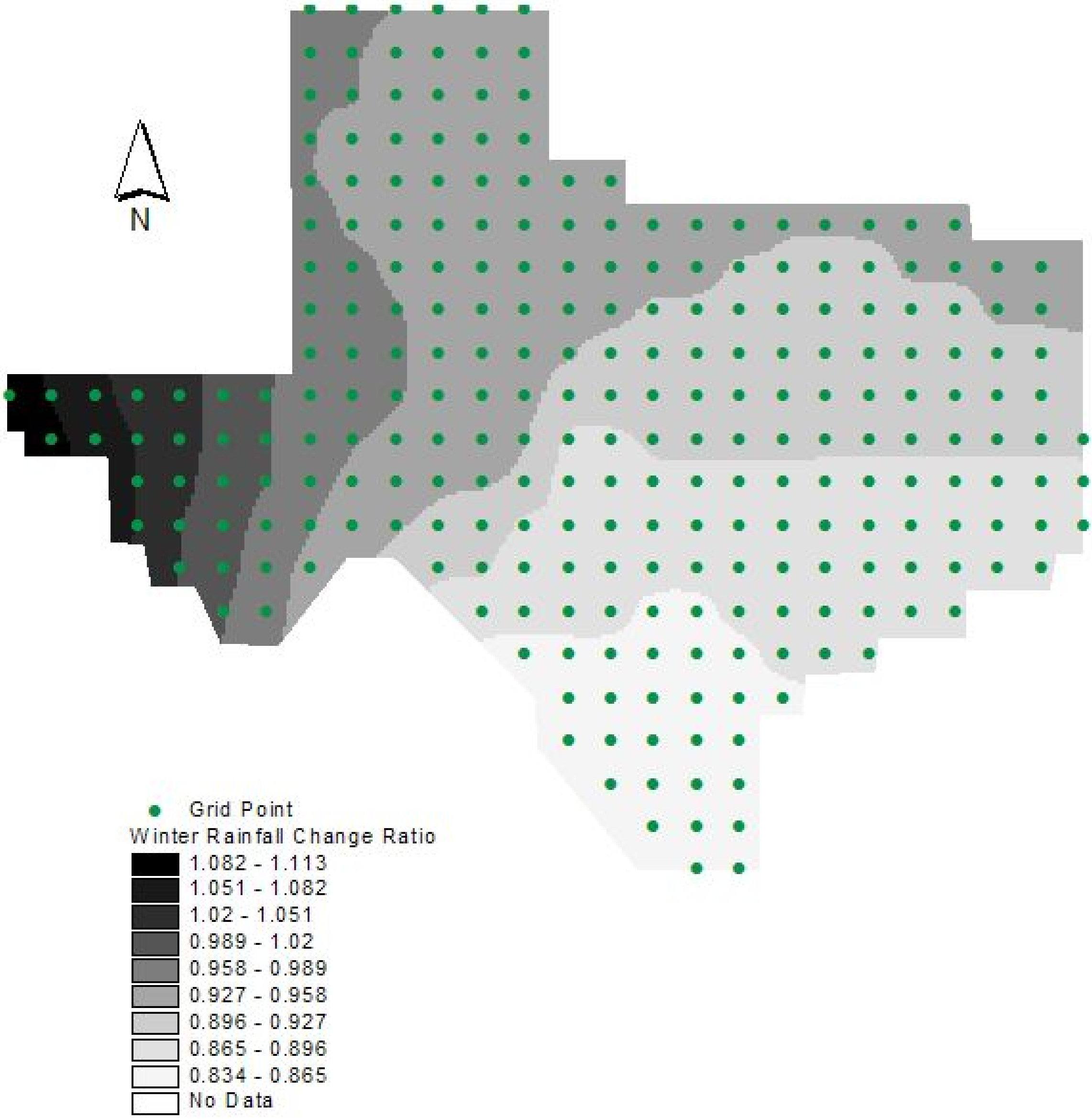

N
Grid Point
Winter Rainfall Change Ratio
1.082 - 1.113
1.051 - 1.082
1.02 - 1.051
0.989 - 1.02
0.958 - 0.989
0.927 - 0.958
0.896 - 0.927
0.865 - 0.896
0.834 - 0.865
No Data

Fig. 7.14. Change in spring rainfall as predicted by the Goddard Institute for Space Science general circulation model for Texas. The values represent the ratio of model predictions at 2×CO_2 and 1×CO_2 concentrations.

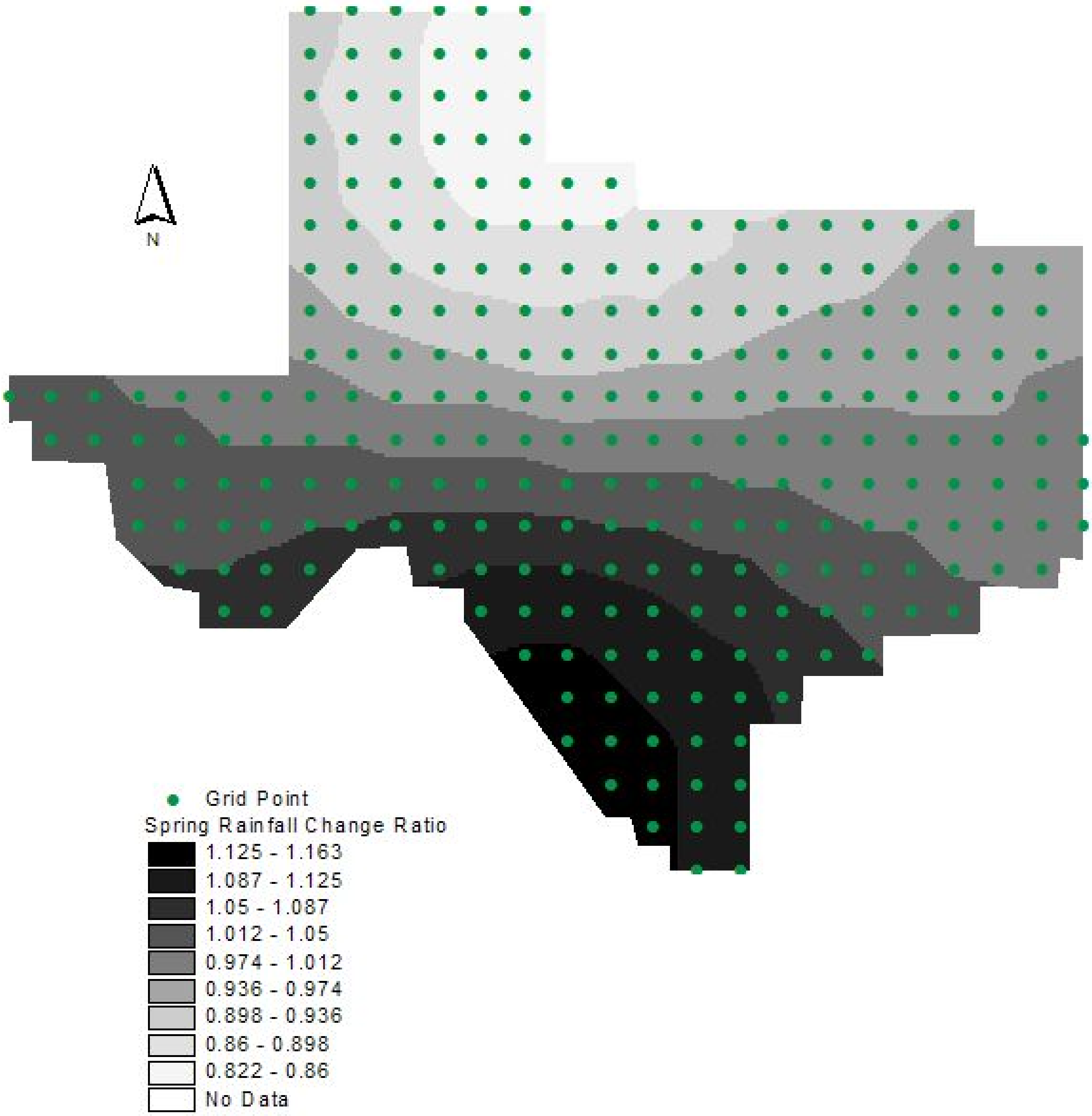

N
Grid Point
Spring Rainfall Change Ratio
1.125 - 1.163
1.087 - 1.125
1.05 - 1.087
1.012 - 1.05
0.974 - 1.012
0.936 - 0.974
0.898 - 0.936
0.86 - 0.898
0.822 - 0.86
No Data

Fig. 7.15. Change in summer rainfall as predicted by the Goddard Institute for Space Science general circulation model for Texas. The values represent the ratio of model predictions at $2\times CO_2$ and $1\times CO_2$ concentrations.

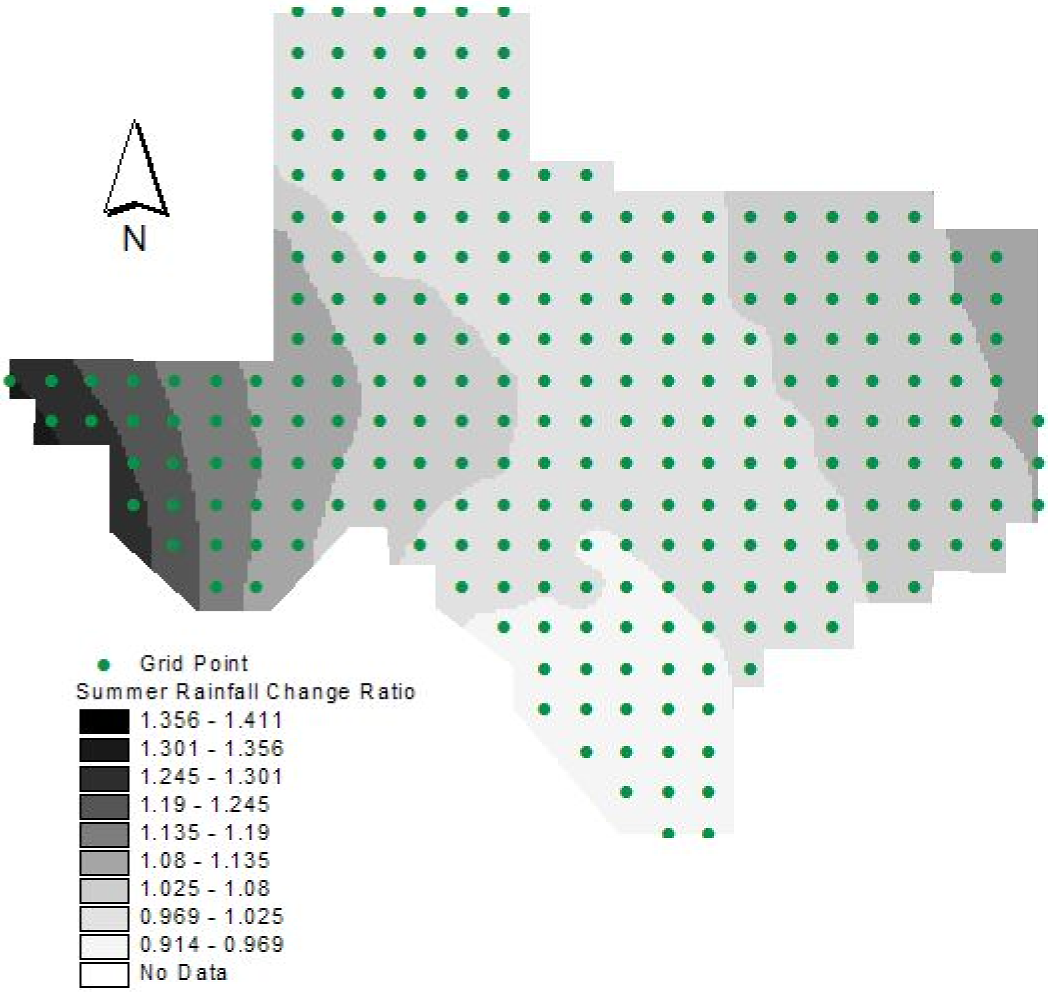
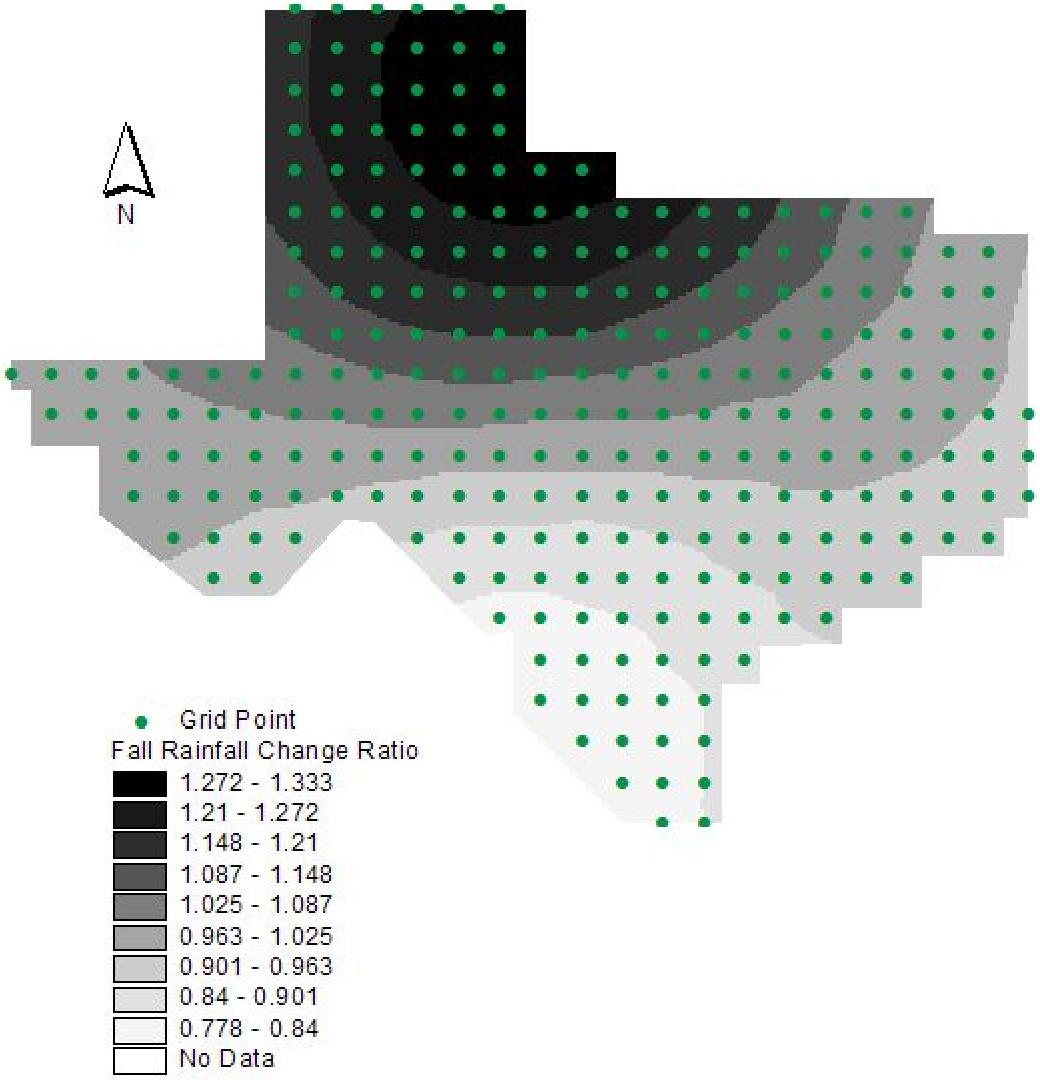

N
Grid Point
Summer Rainfall Change Ratio
1.356 - 1.411
1.301 - 1.356
1.245 - 1.301
1.19 - 1.245
1.135 - 1.19
1.08 - 1.135
1.025 - 1.08
0.969 - 1.025
0.914 - 0.969
No Data

Fig. 7.16. Change in fall rainfall as predicted by the Goddard Institute for Space Science general circulation model for Texas. The values represent the ratio of model predictions at $2\times CO_2$ and $1\times CO_2$ concentrations.


N
Grid Point
Fall Rainfall Change Ratio
1.272 - 1.333
1.21 - 1.272
1.148 - 1.21
1.087 - 1.148
1.025 - 1.087
0.963 - 1.025
0.901 - 0.963
0.84 - 0.901
0.778 - 0.84
No Data

Part of the biotic environment of an animal species is the plant community in which it exists. The responses of plants to global change, therefore, will influence the abundance and distribution of the animals that exploit them, either for food or for shelter (Huntley 1997). Terrestrial plants will respond not only to changes in climate and land use, but also to the increased concentrations of CO_2 in the atmosphere (Woodward 1992). Because CO_2 is an essential component of the photosynthetic process, increased concentrations might increase net primary production (Woodward 1992, Tilman 1993, Bazzaz 1996, Mooney et al. 1999). Grassland ecosystems experimentally exposed to $2\times CO_2$ showed increased mean above ground biomass of approximately 14%, but there was considerable variation in individual species responses, which were dependent on water and nutrient availability (Mooney et al. 1999). The specific species differences in responses might lead to changes in a species' competitive interactions that might further lead to changes in community composition (Davis et al. 1998). Further, the effects of changes in mean daily minimum temperature might differ from the effects of mean daily maximum temperature reported here. For example, Alward et al. (1999) reported that increases in mean daily minimum temperature reduced net primary productivity in a C_4 grass, but increased net primary productivity in C_3 forbs.

In addition to changes in the physiological responses of plants, shifts in species ranges are also expected to occur (Woodward 1987, 1992). A model developed to predict forest-tree distributions under various climate change scenarios indicated that range shifts or range expansions were likely for most species investigated (Iverson and Prasad 1998). The composition of plant communities under global change will, therefore, depend on the individual migration speeds of each species (Iverson and Prasad 1998, Iverson et al. 1999; but see Post 2003), as well as the competitive abilities of each species (Davis et al. 1998). In many cases, the migration speeds of the various plant species will not be sufficient to keep up with the rate of climate change (Peters 1992). Human land-use decisions will complicate the issue, however. In forest ecosystems, tree migration was hampered by fragmentation (Iverson et al. 1999).

The climate-change scenario used here assumed that the proportion of cultivated land and the density of livestock on non-cultivated land would remain at their current mean levels. This is an unlikely assumption, since global change also encompasses change in land cover and land use (Walker and Steffen 1999). Changes include conversion of land to cultivated crops, livestock production, timber harvesting, urban sprawl, and industrial development (Gregory et al. 1999). Landscape changes result from complex interrelationships among population size, economics, socio-political factors, and regional context (Gregory et al. 1999, Walker and Steffen 1999). As the human population grows at an estimated rate of 0.8—1.0 billion/decade (Walker and Steffen 1999), more lands will have to be converted to food production, either through cultivation or livestock production, in order to meet basic food requirements (Gregory et al. 1999). To meet the needs of these growing populations, it is estimated that grain production will have to increase by 32 million ton/year. The amount of area in rangeland or pastureland is also expected to decline as such areas are converted to cultivated cropland (Gregory et al. 1999).

Conversion of rangeland and native vegetation to row crops often converts what was once a heterogeneous landscape into a monoculture. Early agricultural practices typified by many small, family-owned farms, resulted in a pattern of land use referred to as patchwork agriculture. This patchwork was believed to enhance wildlife abundance through the creation of edge between cultivated fields, windbreaks, and fencerows (Leopold 1933). If such land-use changes occur in Oklahoma and Texas, then bobwhite declines predicted here are likely to be conservative.

Changes in climate patterns will affect the flowering phenology of plant species in temperate regions, because seasonal plant phenology is governed by not only photoperiod, but ambient temperature (Galston et al. 1980). The effects of warmer winters and springs on flowering have already been observed. In Washington, D. C., the mean first-flowering times for the local plant community advanced 2.4 days over a 30-year period (Abu-Asab et al. 2001).

The advancement for 89 of the species was highly correlated with increased local minimum temperature.

Changes in seasonal plant phenology can have major impacts on animal species that have evolved life-history characteristics synchronized with these seasonal changes, but that are weakly coupled to actual seasonal changes (Myers and Lester 1992, Root 1993). For example, in many bird species, the timing of breeding coincides with peak food abundance (Gill 1995). However, breeding among these species precedes actual peaks in food abundance and these species must therefore rely on some proximate cue as a signal to begin breeding. As a result, there might be insufficient food available for young once hatched if the proximate cue used by the bird (e.g., photoperiod) no longer accurately signals when the peak in food abundance will occur. Production and, therefore, abundance might be reduced. If the rate of decline in abundance is more rapid than the rate of adaptation to the new climate conditions (i.e., adaptation cannot keep pace with the rate of climate change), populations might become extinct (LaRoe 1991). How much of an effect such a shift in plant phenology will have on bobwhites is unclear. Some species appear to be able to behaviorally adjust the hatch date of their clutches to maintain the synchronization with peak food abundance (Cresswell and McCleery 2003).

Some bird species could be able to track changes in climate better than others, depending on mobility and rate of adaptation. Among many species of birds, the initiation of egg laying has become earlier over the last half century. Of 65 bird species investigated in England over a 25-year period, 31% exhibited trends toward earlier nest initiation, with nests being started an average of 8.8 days earlier (Crick et al. 1997). Only 1 species showed significantly later laying dates (Crick et al. 1997). A later study that spanned 57 years and investigated 36 English bird species found that 38% had trends in long-term nest initiation towards earlier dates and the earlier laying was related to climate change (Crick and Sparks 1999). In the United States, the mean date of first clutch for the Mexican jay (*Aphelocoma ultramarina*) decreased by 10.1 days (Brown et al. 1999). These changes were related to long-term increases in mean minimum monthly temperatures during the onset of the breeding season. The egg-laying date for the North American tree swallow (*Tachycineta bicolor*) advanced by 9 days between 1959 and 1991, and was associated with increases in mean temperature during the breeding season (Dunn and Winkler 1999). These changes in the start of the breeding season might increase the total length of the breeding season for these species, as long as there is not a concomitant changes in the end of the breeding season and increased temperatures do not adversely affect the breeding physiology of the species (Dawson 1992), resulting in higher production. However, temperature is known to adversely affect the breeding physiology of the bobwhite (Klimstra and Roseberry 1975, Guthery et al. 1988). High temperatures during the breeding season can reduce the effective nesting season for bobwhites and increase the rate of nest abandonment (Klimstra and Roseberry 1975). Guthery et al. (1988) reported that gonadal recrudescence began up to 2 weeks earlier and a breeding season 2 months shorter in dry hot environments than in wetter, cooler areas. The percent of hens in breeding condition also declined throughout the summer in south Texas (Guthery et al. 1988).

Global change can affect animal species in a variety of other ways, as well. The arrival date of the American robin (*Turdus migratorius*) on its breeding grounds in the Colorado Rocky Mountains was 14 days earlier in 1999 than in 1981 (Inouye et al. 2000). Distributions of some bird species will shift due to their physiological tolerances and, as noted above, because of changes to the plant communities to which they are adapted. Root (1988) reported that the northern range boundaries of 148 North American bird species were determined by mean minimum January temperature, the length of the frost-free period, and the potential vegetation of the sites. As these environmental conditions change, communities will become disassociated as species migrate to suitable areas at their own individual rates (LaRoe 1991). During this period of flux, new species interactions will occur and some species will be lost. It is clear that in some area of their current range, bobwhites will be lost.

Finally, I offer a caveat on the predicted declines described above. As detailed in the methods section, the GCMs on which predictions were based varied in the assumptions and factors taken into considerations. As a result, the predicted climate patterns under 2×CO_2 concentrations also varied. The predicted declines are, therefore, subject to the assumptions of the underlying GCM. Although the 2 GCMs used in this analysis were qualitatively similar, they were not quantitatively identical. Given this caveat, the predictions presented here are best understood as qualitative. That is, the neural model predictions are useful more for gauging the qualitative changes in abundance than in exactly measuring observed changes.

Aside from underlying differences in GCM structure, the models might also err in their presumption that the climate will reach a new equilibrium state once atmospheric concentrations of CO_2 reach twice 1991 levels. However, the effects of elevated CO_2 concentrations have a level of momentum that will propel climate change for several centuries after the emissions have occurred (IPPC 2001). Therefore, it is likely that the climate will not be stabilized for some time to come, especially if greenhouse gases continue to be added to the atmosphere (IPCC 2001). That is, the GCMs used in this analysis assume that CO_2 levels have doubled and the climate has adjusted to the new CO_2 concentrations.

The results reported here indicate that bobwhite abundances will decline in both Oklahoma and Texas as a result of climate change caused by elevated atmospheric CO_2 concentrations. The exact magnitude of these declines is uncertain and dependent on the underlying GCM used to generate the climate change scenario. However, as climate models continue to be refined, a more realistic depiction of the effects of climate change might emerge. Therefore, these results are a temporary tool for wildlife managers concerned with protecting bobwhite populations as the earth's climate changes.

CHAPTER 8

CONCLUSIONS

The results of the present work, as well as many others, showed the usefulness of the neural network modeling for understanding complex ecological phenomena. I used it to develop predictive models of bobwhite abundance in Oklahoma (Chapters 3 and 4) and Texas (Chapters 5 and 6), and elsewhere to discriminate nest sites from random points for northern bobwhites in Texas (unpublished manuscript) and for lark sparrows (*Chondestes grammacus*) in Oklahoma (Lusk et al. 2003). In each case, my coauthors and I have found relationships among predictor and response variables that would not have been detected using orthodox statistical techniques. In Chapter 3, most of the relationships were non-linear and were missed by the linear regression technique. In fact, one of the chief benefits of neural network modeling is that it does not require a priori specification of the type of relationships (Smith 1996). This feature is useful when little is known about relationships among variables, as is often the case with endangered species, or where there is a strong suspicion that the relationships among predictors and responses are non-linear. Further, neural models offer a method for model selection that is not biased by human preconceptions of the underlying functional relationships. That is, the specification of the functional form of the relationships among predictors and responses is done independently of user input. Although some authors have derided such techniques as "data dredging" (Burnham and Anderson 1999), neural network models can provide hypotheses that can subsequently be tested with empirical data. Neural models also provide methods for discovering ecological patterns within systems where various influencing factors are not given to easy experimental manipulation (e.g., weather) and to cases where vast amounts of data are available (Mitra and Acharya 2003).

Another strength of neural modeling for wildlife management is that it lends itself to an adaptive management approach to conservation. As more information becomes available, the neural models can be updated to provide more accurate predictions. Alternatively, the new data can be used to test the accuracy of the neural models (Chapter 3). In either case, the result is more informed management practices and more effective conservation.

The weather models (Chapters 4 and 5), although not directly comparable because of differences in the type of response variable being modeled, revealed a number of similar response patterns. For example, bobwhite indices (relative abundance, standard normal deviate) declined with increasing June temperatures. In the case of the Oklahoma model, temperatures greater than approximately 31 °C resulted in below average counts, whereas it was mean maximum June temperatures above 33 °C that resulted declines in bobwhite counts in Texas. Similarly, neural models for both states predicted increases in bobwhite counts with increasing July temperatures above approximately 35 °C. Although this result might seem counter intuitive, there are plausible explanations for the results (Chapter 5) dealing with detectablity and the concentration of bobwhites along roadways during hot, dry conditions. Overall, both weather models indicated that summer heat was an important factor in determining fall abundances. Indeed, heat loads high enough to cause the cessation of breeding are commonly experienced by bobwhites in south Texas (Guthery et al. 2001).

The month during which temperatures were most critical varied between the two weather models. In Texas, July temperature was the only variable with a relevance score above 10%. In Oklahoma, temperatures during all 3 summer months were important contributors to the model predictions. It is likely that bobwhite responses to the temporal pattern of summer temperatures vary latitudinally. The further one travels north, for example, the later in the year the onset of high summer temperatures. However, June and August temperatures in Texas neared the arbitrary 10% relevance threshold (8.4 and 7.6%, respectively) and could, therefore, be said to be important variables.

As mentioned in Chapter 1, there is no shortage of studies on the effects of weather and climate on bobwhites. Although response and predictor variables differed among the published studies, the most significant shortcoming is the use of linear analysis methods. It is axiomatic that nature is non-linear. This is because many biological and ecological rates are bounded by definition (e.g., survival bounded by 0 and 1) or by the physical and biological properties of the system (e.g., age ratios of bobwhites). This could be the reason for ambiguous or null relationships among predictors and responses. For example, Edwards (1972) found no relationship between mean monthly temperatures and fall harvest. Further, recruitment was not influenced by mean daily temperature or mean maximum daily temperature in southern Illinois (Roseberry and Klimstra 1984), but age ratios were in south Texas (Guthery et al. 2002).

The weather models also revealed consistent patterns among the land-use variables. In Texas, increasing livestock density decreased bobwhite abundance, whereas in Oklahoma, below average counts attended all but the lowest livestock densities. There were also clear density dependent responses to previous year's bobwhite populations. In Oklahoma, abundance peaked at intermediate previous year's counts and declined with increases in previous year's counts >30 bobwhites. Likewise, in Texas, increases in bobwhite abundance decelerated as previous year's counts increased. The climate-change modeling in Chapter 7 also included land-use variables. However, I made the simplifying assumption that land use under future climate changes would approximate the long-term averages of the variables (Chapter 7). This is likely to be false, since increases in land area under cultivation or dedicated to livestock production will be necessary to support the expanding human population (Gregory et al. 1999)

Another consistency in the results was the finding that climate, measured as the deviation from long-term weather patterns, was a more important determinant of bobwhite abundance than short-term weather patterns (Chapters 4 and 6). This has important implications for understanding the effects of climate change reported in Chapter 7, since temperature and precipitation are both expected to significantly deviate from current conditions (IPCC 2001). As the magnitude of the change in climate increases, so will its effects on bobwhite abundance. This will especially be true if the pace of the changes is more rapid than the adaptive response of the bobwhites to the new local conditions. The reason that climate was a better predictor might be an artifact of the definition of the climate variables. That is, representing climate as deviations from long-term mean conditions might have reduced the noise in the data, allowing the actual weather signal to be more apparent.

The results have practical ramifications for bobwhite management, particularly with respect to management on the current network of wildlife management areas and preserves. Changes in plant and animal communities across the globe are expected due to climate change; lands currently managed as nature preserves and wildlife management areas are no exception. It might come to pass that areas now set aside as prime bobwhite habitat will be uninhabitable when temperatures rise, thus losing their conservation value. These areas might become uninhabitable not only because they are no longer within the climate tolerances of bobwhites, but also because the habitat types associated with the presence of bobwhites might no longer exist under the new climate regime (Dockerty et al. 2003). In fact, there is little consideration given to climate change impacts when management plans are being devised (but see Guthery et al. 2000). Climate change trend analyses in conjunction with the neural models employed here can be used to identify specific sites where bobwhite populations might be able to be maintained (Dockerty et al. 2003), even if at reduced abundance. It might be that no current land holdings will be suitable for bobwhites in 100 years. In such a situation, land-management strategies will likely need to shift focus and more money and effort devoted to acquisition or management of privately held lands.

Unfortunately, no amount of effort will be sufficient to manage climate for some time to come. But, armed with the knowledge of how climate and weather influence bobwhite dynamics, habitat management aimed at ameliorating the effects might prove useful, especially in the short term, It is worth inserting a few words of caution, however. As discussed in Chapter 7, the GCMs used to generate the climate change scenarios are not perfect and include different forcing variables assumed to play roles in climate. Although not perfect, the current generation of GCMs has demonstrated improvement on predicting climate change over a range of spatial and temporal scales (IPCC 2001). The uncertainty in the predicted climate outcomes are magnified when those outcomes are used to predict the responses of various organisms (in this case, bobwhites) using neural models, which themselves have considerable uncertainty associated with them.

In addition to the limitations imposed by the accuracy of the GCMs used in Chapter 7, there are also a limitations imposed by the grain or scale of the GCM predictions. The models used here had a minimum grain size of 0.5 × 0.5°. It is likely that climate change will manifest at a finer scale due to topographic and edaphic factors. The fine-scale details in the predicted responses of bobwhites are thus lost at this scale, but larger-scale patterns still offers managers a picture of what to expect as the climate begins to shift toward a new equilibrium. As more fine-grained GCMs are developed and tested, they can be used to refine our understanding of these processes.

One factor not included in my assessment of the impacts of climate change on bobwhite abundance is catastrophic weather events, such as thunderstorms, tornados, and blizzards and ice storms. Such weather events have been known to cause die offs among bobwhite populations (Errington 1936; Errington and Hamerstrom 1936; Leopold 1937; Scott 1937; Roseberry 1962, 1964). Further, such events are expected to increase in frequency with climate change (NRC 2001, IPCC 1998, 2001). Again, however, weather catastrophes occur at too fine a scale to be obtained from the climate models currently available (IPCC 2001). It will become increasingly important to consider the impacts of weather catastrophes as they become more frequent and their impacts on abundance more persistent.

Given the uncertainties inherent in the available GCMs and in neural models, it is perhaps better that the results of the climate-change scenarios be regarded as possible outcomes and not as predictions. There will undoubtedly be unforeseen impacts of climate change resulting simply from the complexity of the climate system (NAST 2000). Although imperfect, the climate-change results are still useful as a preliminary projection for mitigation planning, especially when considered along with the knowledge gained regarding bobwhite responses to weather factors. Such regional analyses are essential for understanding how climate change will impact the earth's biota, especially since temperature increases in North America could be up to 40% higher than the global mean (IPCC 2001).

CHAPTER 9

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VITA

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