WEATHER AND AGE RATIOS OF NORTHERN BOBWHITES IN SOUTH TEXAS

Fred S. Guthery
Department of Forestry, Oklahoma State University, Stillwater, OK 74078, USA

Jeffrey J. Lusk
Department of Forestry, Oklahoma State University, Stillwater, OK 74078, USA

David R. Synatzske
Texas Parks and Wildlife Department, Artesia Wells, TX 78001, USA

James Gallagher
Texas Parks and Wildlife Department, Artesia Wells, TX 78001, USA

Stephen J. DeMaso
Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, TX 78744, USA

Ronnie R. George
Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, TX 78744, USA

Markus J. Peterson[1]
Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, TX 78744, USA

ABSTRACT

Understanding the effects of weather on quail reproduction in semiarid environments requires simultaneous consideration of temperature and precipitation data. Therefore, we used neural modeling to assess the interactive effects of summer (Jun–Aug) temperatures (monthly means of daily maxima) and seasonal precipitation (totals) on age ratios (juvenile/adult) of northern bobwhites (*Colinus virginianus*) in south Texas based on data collected during 1940–97 (n = 35, 23 years missing). Age ratios increased with June temperature. Ratios were insensitive to mean maximum daily temperature in July up to 36 °C, when they began to decline rapidly. Ratios were insensitive to August temperatures. Ratios increased in an asymptotic manner with fall (Sep–Nov), spring (Mar–May), and summer precipitation, and were least sensitive to fall precipitation and most sensitive to spring precipitation. Based on our analysis, temperature and precipitation influenced bobwhite production in a complex, nonlinear manner that seemed to contain thresholds and asymptotes. Low temperatures can ameliorate the negative effects of drought, and high temperatures can suppress the positive effects of precipitation. The apparent asymptotic effect of precipitation, given temperature, illustrates that assumed linearity between precipitation and production may lead to errors of interpretation and expectation for production in a particular year.

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Key words: age ratio, *Colinus virginianus*, neural modeling, northern bobwhite, precipitation, production, reproduction, temperature, Texas, weather

INTRODUCTION

Annual and seasonal variation in precipitation explains a good deal of the variation in production and abundance of quails in semiarid environments. Kiel (1976) observed that age ratios, an index of production, were a linear function of May–July precipitation in southern Texas. Likewise, precipitation explains a portion of the variation in productivity of scaled quail (*Callipepla squamata*; Campbell et al. 1973), California quail (*C. californica*; Francis 1970); Gambel's quail (*C. gambelii*; Swank and Gallizioli 1954), and Montezuma quail (*Cyrtonyx montezumae*; Brown 1979).

The suppressing effects of high temperatures on reproduction of bobwhites and other quails also are well established, at least in a correlative sense (Leopold 1933, Robinson and Baker 1955, Reid and Goodrum 1960, Speake and Haugen 1960, Stanford 1972). Guthery et al. (2001) provided evidence that annual

[1] Present address: Department of Wildlife and Fisheries Sciences and George Bush School of Government and Public Service, Texas A&M University, College Station, TX 77843

variation in heat loads in the Rio Grande Plains was sufficient to explain boom-bust population behavior of bobwhites in this region. Guthery et al. (2000*b*) hypothesized that global warming could reduce the percentage of hens that attempts to lay, the length of the laying season, and the number of nesting attempts; these reductions would be expected to suppress annual production.

Recently, researchers have addressed the combined effects of temperature and precipitation on production. Heffelfinger et al. (1999) determined that for Gambel's quail in Arizona, the effects of temperature and precipitation were interactive. For example, cooler temperatures could reverse the effects of low rainfall, and hotter temperatures could reverse the effects of high rainfall. Bridges et al. (2001) found that the Modified Palmer Drought Severity Index was a stronger correlate of bobwhite populations than raw precipitation in the South Texas Plains. The Palmer Index incorporates temperature, among other variables, into a precipitation-related variable.

Our objective was to further explore the interactive effects of seasonal precipitation and summer temperatures on bobwhite age ratios in a semiarid environment (South Texas Plains). We used age ratio records collected over a 58-year period and modeled these ratios based on summer temperature maxima (means) and seasonal precipitation. This effort served to place at risk the findings of Heffelfinger et al. (1999). We also developed probability distributions for the weather variables used in modeling so the likelihood of model output could be interpreted.

METHODS

The age ratio (juveniles/adult) data came from Lehmann (1984:133; 1940–1972) and records from the Chaparral Wildlife Management Area (1973–1997; Dimmit and LaSalle counties) operated by Texas Parks and Wildlife Department. Based on large samples (≤18,534), Lehmann's data before 1970 probably came from regional wing collections and were listed only as ''South Texas quail.'' For 1970–1972, his records were from Kiel (1976). All records (Lehmann, Chaparral Area) were based on harvested bobwhites. We deleted 2 outliers (>4 SDs from the mean). With missing values in some years, the data set contained 41 age ratios obtained during 1940–1997.

We used weather records (Earthinfo, Inc., Boulder, Colorado, USA) from Falfurrias and Carrizo Springs, Texas, because these 2 stations had long-term data sets that were complete relative to other potential data sources. To obtain weather data for age ratio modeling, we used weather records from Falfurrias unless records for a particular year were missing, in which case we used records from Carrizo Springs. In some years weather records were missing from both stations. The resulting data set consisted of 35 observations with 32 weather records based on Falfurrias data and 3 on Carizzo Springs data. Variables used in modeling age ratios included mean maximum daily temperatures in June, July, and August, and total precipitation in fall (Sep–Nov of preceding year), winter (Dec–Feb), spring (Mar–May), and summer (Jun–Aug).

We used neural modeling with back propagation of errors (Smith 1996) to develop multivariate models of the age ratio as a function of weather variables. Neural modeling is a powerful, nonparametric method of describing functional relationships. We modeled using commercial software (Neural Connections, SPSS Inc., Chicago, Illinois, USA). The model selected consisted of 7 input nodes (the weather variables), 2 hidden nodes or processing elements, and 1 output node (age ratio). We modeled on 5 randomly drawn subsets of the data (80% of data) to subjectively determine whether modeling on different portions of the data set resulted in similar projected relationships between age ratio and weather variables. Because the projections were generally similar, we report results from the model that yielded the smoothest functional relationships. This model was generated (trained) with 80% of the data, randomly drawn, and tested with the remaining 20% of the data. We generated artificial data and modeled on these data to understand how the age ratio changed with changes in an independent variable. We held other variables constant at their means within the age ratio dataset when modeling the effects of a given independent variable.

We developed beta distributions with parameters estimated by the method of matching moments (Evans et al. 1993) to describe weather features from the Falfurrias station. We used the beta distribution because of its flexibility and simplicity (2 parameters) and because this distribution has served as the basis for stochastic modeling of bobwhite dynamics (Guthery et al. 2000*a*). The probability distributions presented here could be used in the Guthery et al. (2000*a*) model. The weather data were collected over 1908–1997 with 11 years missing ($n = 79$). An outlier for fall precipitation was removed, resulting in $n = 78$ for that season. Also, the beta distribution failed to adequately describe June temperature records, so we used the normal distribution for this month.

RESULTS

The linear correlation between observed age ratios and those predicted by the neural model was $r = 0.77$ ($n = 28$) for the training data and $r = 0.55$ ($n = 7$) for the validation data. When the model was applied using mean values for all weather variables, it predicted an age ratio of 2.21 juveniles/adult, which compared with the mean estimated from the data of 2.45 ± 0.29 (SE) juveniles/adult. These results indicated the neural model identified relationships in the data, but that a large percentage of variation in the data remained unexplained.

The simulated relationships between the age ratio and temperature and precipitation variables were developed on the same *x*–y scales (Figs. 1 and 2) so that sensitivity of age ratio to a variable could be estimated by the ranges of predictions (larger range, more sen-

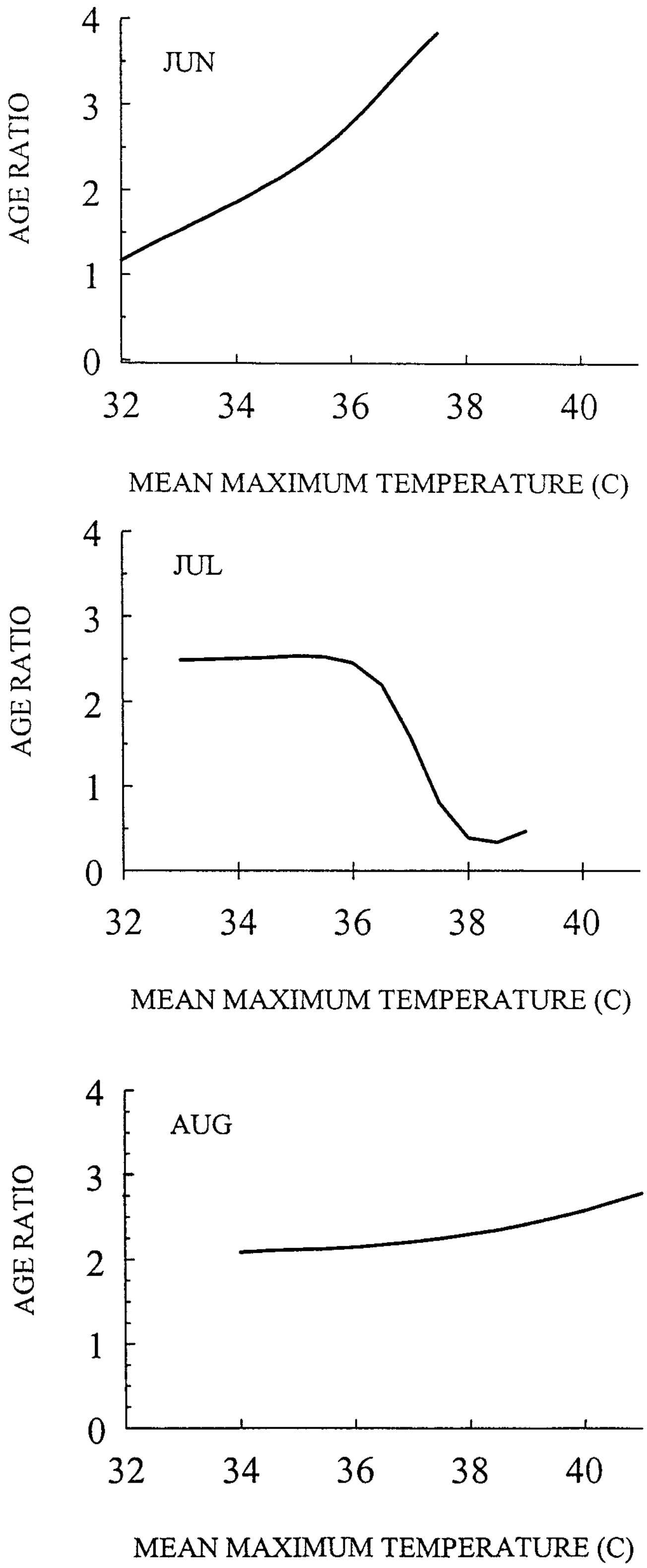

Fig. 1. Neural model predictions of northern bobwhite age ratios in south Texas as a function of mean maximum temperatures in June, July, and August during 1940–1997 (23 years missing). The predictions were generated for any 1 variable by holding values for other variables constant at their means in the dataset. Independent variables included mean maximum temperatures and precipitation (mm) for winter, spring, summer, and fall.

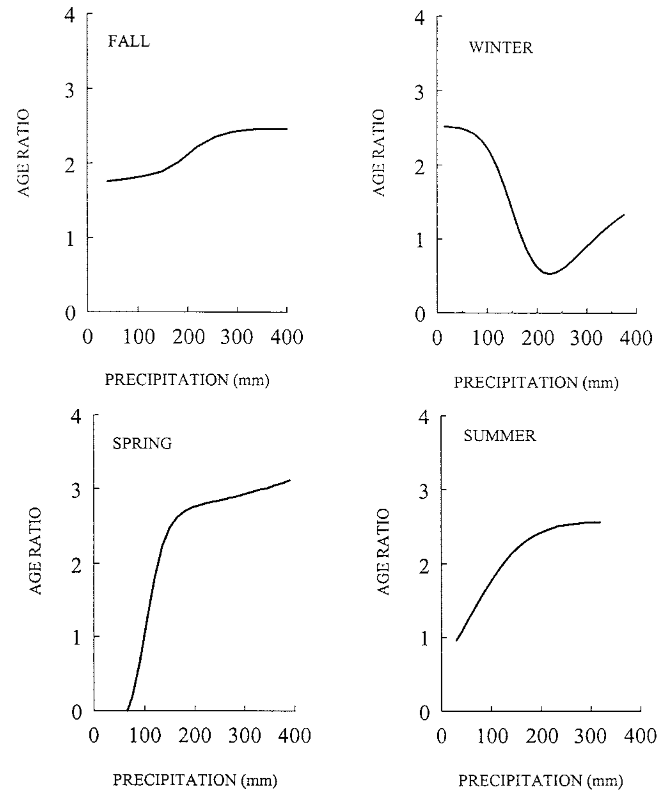

Fig. 2. Neural model predictions of northern bobwhite age ratios in south Texas as a function of total seasonal precipitation during 1940–1997 (23 years missing). The predictions were generated for any 1 variable by holding values for other variables constant at their means in the dataset. Independent variables included mean maximum temperature in June, July, and August and precipitation for winter, spring, summer, and fall.

sitivity). With other variables held constant at their means, the age ratio increased with June maximum temperatures within the range of observed values (32–38 °C). For July temperatures, however, the ratio was insensitive to temperature up to a threshold of about 36 °C, at which point productivity seemed to collapse. There was a weak tendency for the age ratio to increase with August temperatures, but the ratio was insensitive to August temperatures in comparison with June and July temperatures.

The relationships between seasonal precipitation and the age ratio revealed a common pattern for fall, spring, and summer precipitation: the age ratio increased curvilinearly and monotonically with precipitation and the ratio was somewhat insensitive to higher quantities of precipitation (Fig. 2). In other words, the rate of increase in the age ratio decelerated with increasing amounts of precipitation, resulting in an approximate asymptote for fall and summer precipitation. The modeled response to winter precipitation was a complex, curvilinear effect with high predicted ratios at low and high amounts of winter precipitation and the low predicted ratio at intermediate amounts. The age ratio appeared to be least sensitive to fall precipitation and most sensitive to spring precipitation.

Because the age ratio seemed sensitive to July temperatures and spring precipitation, we plotted mod-

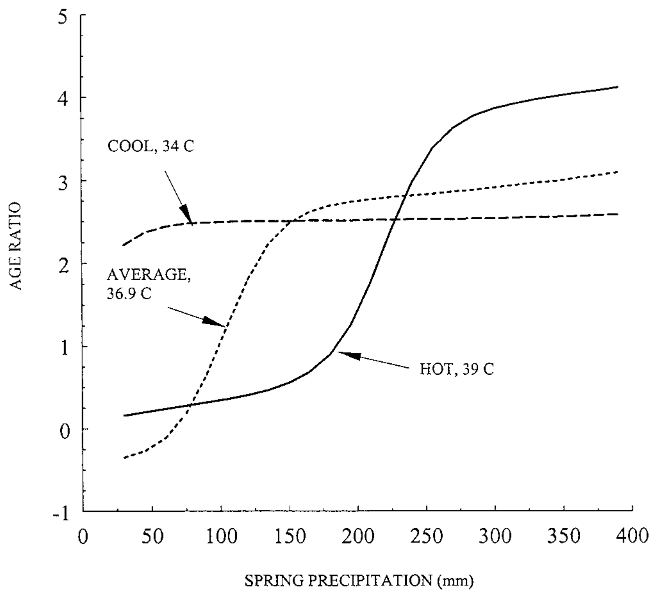

Fig. 3. Neural model predictions of northern bobwhite age ratios in south Texas as a function of spring precipitation and July temperatures (mean maximums, °C) during 1940–1997 (23 years missing). The predictions were generated by holding mean maximum temperatures in June and August and total precipitation in winter, summer, and fall constant at their means in the dataset.

el predictions at 3 arbitrary July temperatures as a function of spring precipitation (Fig. 3). This is a method of perceiving different portions of a multidimensional response surface in 2 dimensions; the remaining variables were held constant at their means. During cool Julys, the age ratio was insensitive to the amount of spring precipitation and tended to be above average. The ratio increased in a logistic fashion when mean maximum temperatures in July were average. At spring precipitation values exceeding 150 mm, the age ratio was somewhat insensitive (increased at a slow rate) to increasing precipitation. A similar, logistic-like effect was estimated for hot Julys, but peak production occurred at about 275 mm (10.8 inches) of spring precipitation and then stabilized.

The results given above need to be interpreted in the context of the probabilities associated with weather events that may inhibit or foster production as indexed with an age ratio. For example, even if cool temperatures in July could override the effects of low spring rainfall (Fig. 3), such temperatures would occur with low probability (Fig. 4). Mean maximum July temperatures below 34 °C were estimated to occur in 3 of every 100 years, whereas means below 35 °C were estimated to occur in 15 of every 100 years. Consider also the high age ratios predicted for hot Julys with high amounts of spring precipitation (Fig. 3). July temperatures equaling or exceeding 39 °C with spring rainfall exceeding 300 mm (11.8 inches) were estimated to occur in 2 of every 1,000 years, if spring rainfall is independent of July temperatures. This expected frequency is based on the product of probabilities from the July temperature (Fig. 4) and spring precipitation (Fig. 5) probability distributions.

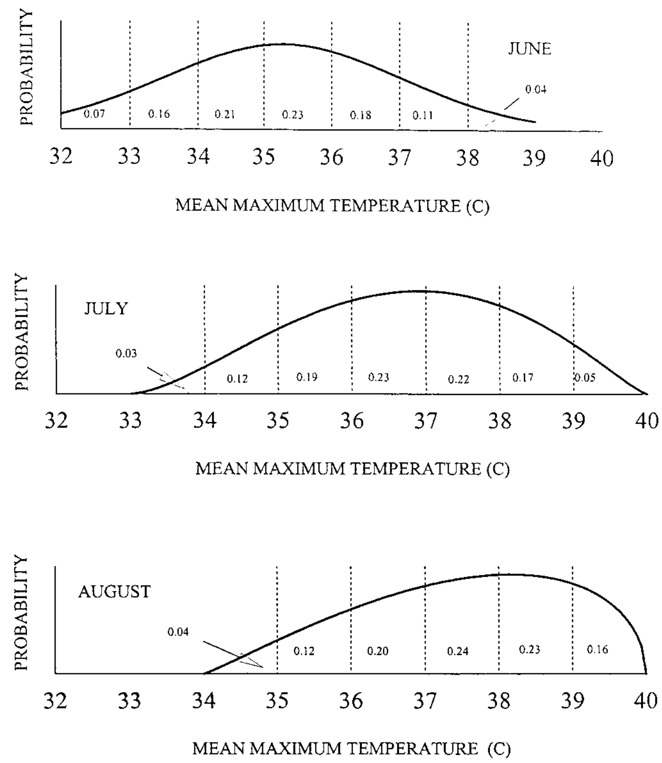

Fig. 4. Estimated probability distributions for mean maximum temperatures in south Texas for June, July (α = 2.5880, β = 2.2470), and August (α = 2.1145, β = 1.4954) during 1908–1997 (11 years missing; Falfurrias station). Numbers under the curves give approximate probabilities that mean maximum temperatures fall within the indicated range. June temperatures were modeled under the normal distribution ($\bar{x}$ = 35.3, SD = 1.77) because off a poor fit to the beta distribution; probabilities reflect the normal distribution truncated to the range of observed temperature values.

DISCUSSION

Throughout this manuscript we have discussed the age ratio as an index of production. We acknowledge that it may be an ambiguous index because an age ratio is a complex function of 9 demographic variables and 1 function (Guthery and Kuvlesky 1998). This complexity means that there are many demographic and time-based processes that may lead to the same age ratio. Other indices of production, such as the percentage of juveniles in a population or percent summer gain, are equally ambiguous. This statement is true because age ratio, percent juveniles, and percent summer gain are mathematically related such that any one can be derived from any other (Guthery 2002). Converting the age ratio or percent juveniles to percent summer gain requires knowledge of breeding-season survival of adults. Otherwise, all of the production indices discussed above depend on the same driving variables. So any commonly applied index of production contains the same ambiguity because all are tautologically equivalent.

Weather (temperature, precipitation) alters age ratios through effects on demographic variables such as the probability of nest success, proportion of hens that lays, number of nesting attempts per hen, clutch size,

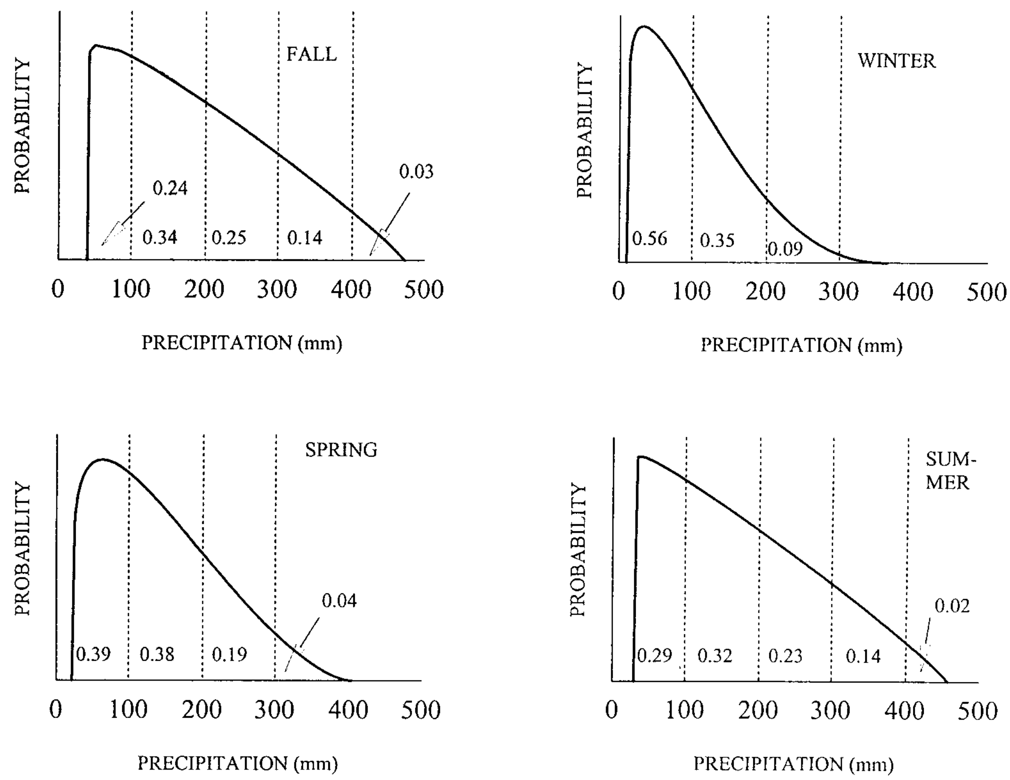

Fig. 5. Estimated beta distributions for seasonal precipitation in south Texas for fall ($\alpha = 1.0342$, $\beta = 1.9060$), winter ($\alpha = 1.1467$, $\beta = 3.3001$), spring ($\alpha = 1.1944$, $\beta = 2.6173$), and summer ($\alpha = 1.0161$, $\beta = 1.9073$) during 1908–1997 (11 years missing; Falfurrias station). Numbers under the curves give approximate probabilities that precipitation falls within the indicated range.

length of the laying season, seasonal distribution of nest initiation, and survival of adults and juveniles, among others. Our modeling effort was an attempt to synthesize weather influences on the complex demographic and dynamic influence leading to an age ratio. The effort necessarily required simplification that resulted in some level of mismatch between the variables used in modeling and the reality of the field. For example, we assumed data from the Falfurrias station reflected conditions for the region of inference. Also, modeling an age ratio on means (temperatures) and totals (precipitation) fails to account for the frequency, pattern, and intensity of weather events. A given mean maximum temperature might or might not be associated with intense heat waves, and a particular total for precipitation might or might not have accrued from a deluge. Because of the complexity of an age ratio per se and variation quashed by modeling on means and totals, the neural model predictions were associated with considerable uncertainty. The model performed with at best moderate predictive power (explained 59% of variation in training data, 29% in validation data).

A model with the specified level of performance should be viewed with skepticism, especially since it was developed with a relatively small sample ($n = 35$). However, such a model may contain useful information if it is consistent with known weather-related processes affecting quail production. Also, such a model, given empirical support, may be informative if it suggests patterns or processes that have gone undiscovered in previous work.

Certain aspects of the model predictions were consistent with published results. Our analysis identified spring precipitation as a key variable influencing age ratios, as did Kiel's (1976) work in the same region. In contrast to Kiel (1976), however, our analysis suggested an asymptotic effect of spring precipitation, whereas his findings were linear over age ratios ranging from 0.6 to 7.0 (we would have eliminated the higher age ratio as an outlier). The asymptotic effect seems more realistic, biologically, than the linear effect. Theoretically, the age ratio is an asymptotic function of the number of nesting attempts (Guthery and Kuvlesky 1998), and the number of attempts in any breeding season is time-limited. This would lead to the expectation, if precipitation lengthens the breeding season and thus increases the potential number of nesting attempts, that production could be an asymptotic function of precipitation.

Our results were consistent with the findings of Heffelfinger et al. (1999) concerning weather effects on age ratios of Gambel's quail in Arizona. They reported that mid-winter (Dec–Jan) precipitation was more influential than early-winter (Oct–Nov) or late winter (Feb–Mar) precipitation. Although we found spring rainfall to be more important than rainfall in other seasons, the Arizona and south Texas results were consistent if timing of rainfall is placed in phenological context. Gambel's quail in Arizona start nesting before bobwhites in south Texas; the common property between studies was the importance of rainfall associated with the beginning or early portions of the nesting season. Heffelfinger et al. (1999) reported declining age ratios with increasing July temperatures, regardless of the quantity of rainfall. On the contrary, we observed a threshold effect of July temperature at a given rainfall (Fig. 1). However, the results were consistent in that higher July temperatures were associated with lower predicted age ratios in each study.

The threshold effect of July temperatures and other results were consistent with known aspects of the thermal biology of bobwhites. Heat stress, as evidenced by gular flutter, appears at a temperature of about 35 °C in quails (Henderson 1971, Spiers et al. 1983). The model predicted a collapse in production at a mean maximum temperature of about 36 °C in July (Fig. 1). A possible process leading to a collapse in production at temperatures near 35 °C is reproductive quiescence associated with heat stress. In contradiction, however, the model predicted increasing age ratios with increasing June maxima beyond the threshold value. These results were enigmatic. The age ratio essentially failed to respond to August temperature maxima, which may merely indicate most production has completed before August. We recognize that bobwhites may lay during any month in south Texas (Lehmann 1984:84) but this occurrence does not preclude a strong seasonal peak in reproduction effort (Guthery et al. 1988). Based on data presented in Guthery et al. (1988), the breeding effort essentially collapses by July in the western Rio Grande Plains and is in strong decline in the eastern Rio Grande Plains. Data from the Chaparral Area were reflective of the western Rio Grande Plains.

Rainfall in semiarid environments generally benefits birds and, with the exception of winter precipitation, this generalization held for bobwhite age ratios in south Texas (Fig. 2). We can speculate that winters with more precipitation are colder, leading to energy stress that inhibits early season production. Indeed, Koerth and Guthery (1988) reported that body fat levels of bobwhites in April were negatively correlated with total precipitation the preceding February for the south Texas region. This conjecture would be consistent with declining age ratios with increasing winter precipitation up to about 225 mm (8.9 inches). However, we cannot explain why predicted production would increase as rainfall increased above 225 mm. The result may simply represent an anomaly in the dataset.

We have tried to identify the deficiencies in the data set we analyzed and readers should keep these deficiencies in mind as we conclude with some generalizations. We observe, first, that quail production in semiarid environments appears to respond to both temperature and precipitation. It is conceivable, based on empirical data (Heffelfinger et al. 1999, this study), that lower temperatures can ameliorate the negative effects of drought on production. Moreover, higher temperatures can suppress the positive effects of precipitation. The weather-quail production system seems to be nonlinear with thresholds and asymptotes. Obviously, nonlinearity renders linear outlooks on the weather-production relation incomplete and, in certain domains of inference, inaccurate. For example, if the production response to precipitation is approximately asymptotic (Fig. 2), then there are precipitation levels that invoke a null response in quail productivity. There is a tendency for human beings to linearize and simplify, which likely will lead to false expectations of bobwhite population performance in the system we studied.

MANAGEMENT IMPLICATIONS

The weather is beyond management control. However, knowledge of the nature and strength of weather influences on bobwhite demography assists managers in placing proper perspectives on practices aimed at enhancing the reproduction performance of quail in semiarid environments such as south Texas. Weather variables may explain at least half, and perhaps more, of the variation in bobwhite age ratios in south Texas (Kiel 1976, this study). Adding random variation associated with depredation events (nest, chick, adults) and other limiting factors to the variation explained by weather leaves little room for variation explained by habitat management practices. Moreover, the power of weather suggests that such practices should be aimed primarily at ameliorating the negative reproduction effects of low rainfall in association with high temperatures. Management for positive thermal effects involves preservation of adequate amounts of herbaceous and woody cover to reduce heat loads near the ground and provide thermal refugia (Guthery et al. 2001). In the absence of prohibitively costly measures such as widespread sprinkler irrigation, it is likely that management never will be able to fully reverse the effects of weather on reproduction because the habitat structure to which quail are adapted renders them vulnerable to thermal insult.

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