INFLUENCE OF PRECIPITATION TIMING AND SUMMER TEMPERATURES ON REPRODUCTION OF GAMBEL'S QUAIL

JAMES R. HEFFELFINGER,[1] Arizona Game and Fish Department, 555 North Greasewood Road, Tucson, AZ 85745, USA
FRED S. GUTHERY, Department of Forestry, Oklahoma State University, Stillwater, OK 74078, USA
RONALD J. OLDING, Arizona Game and Fish Department, 555 North Greasewood Road, Tucson, AZ 85745, USA
COLLINS L. COCHRAN, JR.,[2] Arizona Game and Fish Department, 555 North Greasewood Road, Tucson, AZ 85745, USA
CRAIG M. McMULLEN, Arizona Game and Fish Department, 555 North Greasewood Road, Tucson, AZ 85745, USA

Abstract: We analyzed the influence of rainfall and temperature patterns on Gambel's quail (*Callipepla gambelii*) to better understand variability in call counts and reproduction. Based on data collected in Arizona during 1978–96, midwinter (Dec–Jan) precipitation invoked a stronger calling response than early-winter (Oct–Nov) or late-winter (Feb–Mar) rainfall. Reproductive failure (<1 juv/ad) was associated with low rainfall in October–March and high mean daily temperatures during June–July. Moderate production (1–2 juv/ad) occurred under low rainfall in winter, if June–July temperatures were cool. For any rainfall pattern, higher temperatures in July were associated with lower age ratios.

Populations of quail in semiarid environments respond demographically to weather variables, particularly seasonality and quantity of precipitation. Populations tend to adapt to the prevailing regional climates (Campbell et al. 1973), so the relation between weather variables and demography of quail differs among regions. Generally, however, rainfall during key periods directly or indirectly promotes productivity in semiarid environments (Lehmann 1953, Swank and Gallizioli 1954, Gullion 1960, Francis 1970, Campbell et al. 1973, Botsford and Brittnacher 1992). Properly timed rainfall may also foster higher survival (Brown 1989).

An index of production (juv/ad) of Gambel's quail in Arizona increases with precipitation during December–April (Swank and Gallizioli 1954). Calling activity, which apparently varies with breeding density and intensity of the breeding effort (Hungerford 1960), also predicts hunter success (Smith and Gallizioli 1965). Variability in calling activity is associated with variability in precipitation.

Despite general knowledge of the relation between rainfall and the behavior and population dynamics of Gambel's quail, certain key features of this relation remain unknown. Our purpose was to determine how the pattern (timing, amount) of rainfall affects an index of production (juv/ad) in Gambel's quail. We also explored the effects that temperatures during the brooding season had on production, because of the possible effects of global climate change on populations of quail (Guthery et al. 1999).

[1] E-mail: cervidnut@aol.com
[2] Present address: Box 714, Oracle, AZ 85623, USA.

STUDY AREA

Data for this study were collected from 1978 to 1996 near Oracle Junction in southcentral Arizona, about 45 km north of Tucson in Pinal County. Vegetation is characteristic of the Arizona Upland subdivision of the Sonoran Desert Scrub and Semidesert Grassland (Brown 1994). Terrain is flat to gently rolling, and mean annual rainfall at San Manuel, Arizona, (25 km east of the study area) was 37.1 cm (National Oceanic and Atmospheric Administration 1996). Brown et al. (1978) described the study area in detail.

METHODS

We established 2 standardized routes on the study area: 1 on Freeman Road and another on Willow Springs Road. We conducted call counts along each route at 2-week intervals as described by Smith and Gallizioli (1965), starting the last week in March in each of 19 years (1978–96). The analysis of call counts excluded data from 1988 because these data were collected differently and considered unreliable.

Each call count consisted of a 32-km survey route. Beginning 15 min before sunrise, the observer traveled along the route at 40 km/hr and stopped every 1.6 km to count the number of single-note calls of male Gambel's quail during a 3-min period. These "cow" calls are characteristic of male Gambel's quail in breeding condition. The total number of calls heard along the entire 32-km route yielded a call-count index. Call counts were not conducted if rain was falling or wind velocity exceeded 12 km/hr at any time during the survey. Each year, ≥3 call counts were conducted on each route; if the third count recorded the highest total calls, a fourth was completed to reduce the possibility of missing the peak in the calling period. The dependent variable used in this study was the mean of the second and third counts.

Check stations were established in both the Freeman Road and Willow Springs Road sites and operated during the opening weekend of the quail season in October 1978–96. Until 1990, check stations were mandatory for all hunters leaving the area. Since that time, check stations were voluntary, but hunters rarely passed without stopping. All Gambel's quail were aged as adults or juveniles via coloration of the upper primary coverts (Brown 1989). Because the Freeman Road and Willow Springs Road check stations were operated on the call-count routes, the birds checked were from the same areas sampled with call counts. Willow Springs and Freeman roads were the main access to the study sites; hence, we could sample most hunters and their harvest during the times check stations were in operation. The mean number of birds aged each year from 1978 to 1996 was 418 (range = 45–1,530) at Freeman Road and 824 (range = 118–2,464) at Willow Springs.

We used neural network (backpropagation) modeling (Kosko 1992, Anderson 1995, Hagan et al. 1996, Smith 1996) to explore the relation between weather variables and an index to reproduction of Gambel's quail (NeuralWorks Professional II/Plus, Version 5.3). Neural models were developed to mimic the thought processes of humans, and the terms used in neural modeling may be similar to those used in neural biology.

The type of neural network model used here, called the backpropagation model, consists of input nodes (= independent variables), hidden nodes, and output nodes (= dependent variables), and deals inherently with nonlinear relations. Although different architectures are available for backpropagation models, all input nodes are generally connected to all hidden nodes, and all hidden nodes are connected to all output nodes. The connections (synapses) are bridged by linear models governed by synaptic weights. Hidden nodes are also called processing elements because they are loci for input from input nodes, transformation of the input, and output to the output nodes.

Backpropagation modeling is an iterative approach to finding the global minimum on a multidimensional error surface (the method cannot guarantee that the global minimum is found). Basically, a set of synaptic weights (analogous to linear regression coefficients) for synaptic connections between nodes is tested on a set of data, and the unexplained error is calculated. The weights are then adjusted according to learning rules; adjustments take place such that the unexplained error declines (a lower point is found on the multidimensional error surface). This process is repeated until the unexplained error stabilizes or reaches an acceptable value. A backpropagation model finds an approximation for some unknown function as the sum of a series of terms. In this sense, neural models are similar to series expansions (e.g., the Fourier series and the Taylor series). Smith (1996)

provides a readable explanation of backpropagation modeling vis-a-vis traditional modeling such as multiple regression.

The independent variables (input nodes) were monthly records of temperature from the Florence Station (40 km northwest of study area) and records of rainfall from the San Manuel Station (National Oceanic and Atmospheric Administration 1978–96). We used the data from Freeman Road for training the networks (finding synaptic weights that minimized error), and we used the data from Willow Springs Road for testing models developed from the Freeman data. Training sessions involved 100,000 epochs of 16 iterations. This statement means errors accumulated over 16 iterations and synaptic weights were adjusted 100,000 times. The test data were not ideal, because the same independent variables were used in the training and test data. However, we had independent estimates of the dependent variables (call-count index, age ratios).

Our general approach was to experiment with data from Freeman Road, going from more complex (more input nodes and hidden nodes) to less complex models until we found a less complex model that explained >25% of the variation in the call-count index or the age ratio. For call-count modeling, we started with 6 input nodes (monthly rainfall during Oct–Mar) and 6 hidden nodes. We started with 9 input (monthly rainfall and mean daily temperatures in May, Jun, Jul) and 6 hidden nodes for the age-ratio model. Simplification of the models was limited by our objective, which was to determine the effects of rainfall patterns on an index to reproduction (i.e., if models became too simple, we would lose the ability to analyze for pattern effects).

The call-count index for Willow Springs was related to the index for Freeman Road according to

$$Y = 442.7 + 0.4X,$$

where Y = the Willow Springs index and X = the Freeman index ($r = 0.70$, $P < 0.001$, $n = 19$). Therefore, predictions of Willow Springs counts based on a neural network trained with data from Freeman Road were guaranteed to be erroneous because the intercept differed from zero and the slope differed from 1. We adjusted the Willow Springs counts to the Freeman standard by solving for X in the above equation (i.e., $X = Y/0.4 - 442.7$). This variable

(X) was used in testing the Freeman model on the data from Willow Springs. Adjustments were not necessary for the age ratio models because age ratios are standardized as juveniles/ adults (JPA). Moreover, the age ratios between areas were related, with intercept = 0 and slope = 1 ($P > 0.05$) when an outlier (discussed later) was removed from the dataset.

We pooled the data from Freeman and Willow Springs to develop a general neural network model for the age ratios after validating the Freeman model on data from Willow Springs. This pooled model and the model developed for the call-count index were used to predict call counts and age ratios under a comprehensive dataset created to provide a general perspective of the response of Gambel's quail to weather variables (essentially, we modeled with the neural models). The created dataset allowed us to explore model predictions (response surface in hyperspace) by holding certain independent variables constant and manipulating others. In this manner, we could examine the influence of rainfall patterns on calling activity and production. We constrained the arbitrary dataset within about 2 standard deviations of mean weather variables with means estimated over 1978–96. All means are presented ± SD.

RESULTS

Predicting Call Counts

For further testing, we selected a neural network model consisting of 3 input nodes (total rainfall in 3 2-month periods: Oct–Nov, Dec–Jan, and Feb–Mar), 2 hidden nodes, and 1 output node (call-count index). This model explained 73% ($P < 0.001$) of the variation in the data from Freeman Road and 30% ($P < 0.001$) of the variation in the adjusted data from Willow Springs Road when applied to those data (Fig. 1). The empirical data revealed a pooled mean of 1,976 ± 1,027 calls/route, whereas the mean of model predictions was 1,705 ± 652 calls/route.

The neural model predicted a marked response of calling males to rainfall pattern. Analysis of model predictions (Table 1) suggested responses of about 15–25 calls/cm for October–November precipitation, 90–100 calls/cm for December–January precipitation, and 50–65 calls/cm for February–March precipitation. These ranges include drier and wetter years. Thus, in terms of the stimulating effects of a
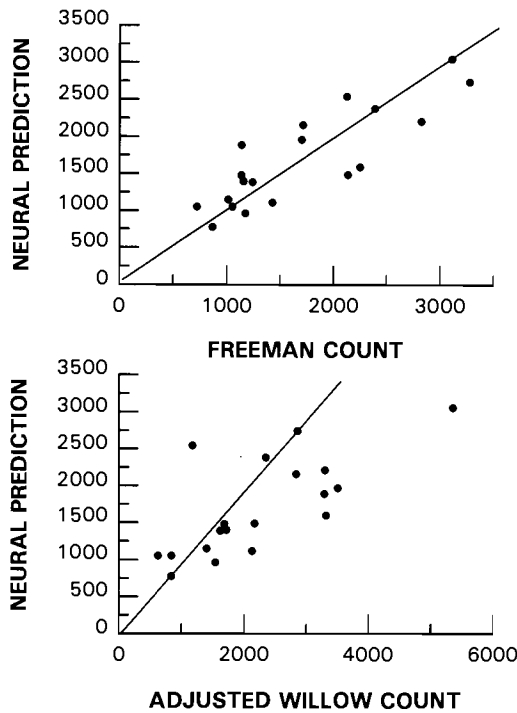
FREEMAN COUNT

ADJUSTED WILLOW COUNT

Fig. 1. Comparisons of neural network predictions of a call-count index of Gambel's quail and actual counts in southcentral Arizona, 1978–96. The top figure shows Freeman Road predictions for a model trained with Freeman Road data, and the bottom figure shows Willow Springs predictions for the Freeman-trained model. All observations would fall on the diagonal line if the model predicted the call-count index perfectly.

Table 1. Neural model predictions of call-count indices for Gambel's quail in response to rainfall patterns based on data collected in southcentral Arizona, 1978–96.

Precipitation (cm)			Predicted calls	Intensity index[a]
Oct–Nov	Dec–Jan	Feb–Mar		
0.0	0.0	0.0	498	0.14
0.0	0.0	6.3	755	0.21
0.0	0.0	12.7	1,084	0.30
0.0	0.0	19.0	1,480	0.41
0.0	6.3	0.0	949	0.26
0.0	12.7	0.0	1,572	0.43
0.0	19.0	0.0	2,284	0.63
6.3	0.0	0.0	590	0.16
12.7	0.0	0.0	691	0.19
19.0	0.0	0.0	802	0.22
6.3	6.3	6.3	1,476	0.41
12.7	12.7	12.7	2,765	0.76
19.0	19.0	19.0	3,623	1.00

[a] Estimated call-count index divided by the maximum estimated call-count index (3,623).

the mean derived from model predictions was 2.0 ± 0.79 JPA.

One observation on Freeman Road in 1991 (6.7 juv/ad) was 3.8 standard deviations from the mean, indicating an unlikely ratio. For that
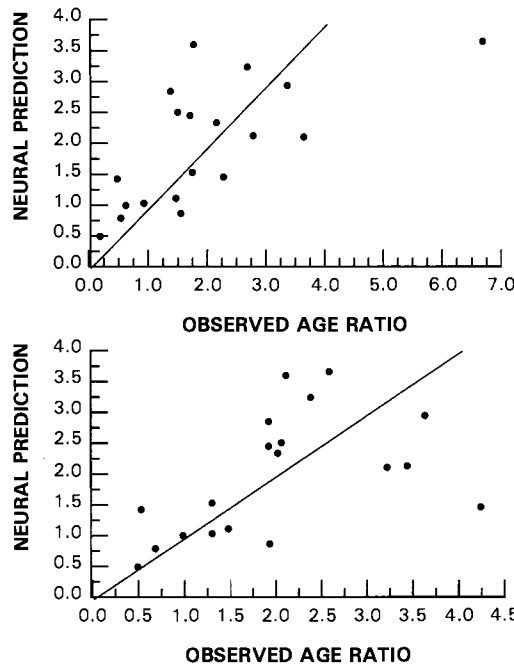
fixed quantity of precipitation on calling behavior, December–January > February–March > October–November.

Model predictions also showed that calling intensity did not increase in proportion to rainfall. For example, doubling (2X) October–November rainfall (holding other months at zero) resulted in a 1.17X increase in the predicted call-count index, whereas doubling December–January rainfall produced a 1.66X increase. Doubling February–March rainfall produced a 1.44X increase.

Predicting Age Ratios

A neural model with 6 input nodes (total rainfall for Oct–Nov, Dec–Jan, Feb–Mar; mean daily temperature for May, Jun, Jul) explained 30.1% ($P = 0.002$) of the variation in age ratios from Freeman Road; the Freeman model explained 25% ($P = 0.029$) of the variation in age ratios from Willow Springs (Fig. 2). The mean age ratio pooled over the Freeman and Willow Springs study sites was 2.0 ± 1.24 JPA, whereas

OBSERVED AGE RATIO

OBSERVED AGE RATIO

Fig. 2. Comparisons of neural network predictions of age ratios (juv/ad) of Gambel's quail and actual ratios in southcentral Arizona, 1978–96. The top figure shows Freeman Road predictions for a model trained with Freeman Road data, and the bottom figure shows Willow Springs predictions for the Freeman-trained model. All observations would fall on the diagonal line if the model predicted the age ratios perfectly.
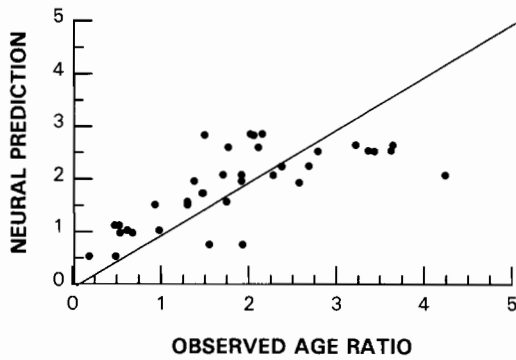
Fig. 3. Comparison of neural network predictions of age ratios (juv/ad) of Gambel's quail and actual ratios in southcentral Arizona, 1978–96. The neural model used to develop the predictions was trained on pooled data from Freeman Road and Willow Springs with an outlier (6.7 juv/ad) deleted. All observations would fall on the diagonal line if the model predicted age ratios perfectly.

Table 2. Neural model predictions of age ratios (juv/ad) of Gambel's quail in response to rainfall patterns based on data collected in southcentral Arizona, 1978–96. Mean daily temperatures were held constant at 23.9°C in May, 29.4°C in June, and 32.2°C in July for these simulations.

Total precipitation (cm) for 2 months			Predicted age ratio
Oct–Mar	Dec–Jan	Feb–Mar	
0.0	0.0	0.0	0.5
0.0	0.0	6.3	0.8
0.0	0.0	12.7	1.1
0.0	6.3	0.0	1.0
0.0	6.3	6.3	1.4
0.0	12.7	0.0	1.7
0.0	12.7	12.7	2.4
6.3	0.0	0.0	0.8
6.3	0.0	6.3	1.1
6.3	6.3	0.0	1.4
6.3	6.3	6.3	1.8
12.7	0.0	0.0	1.2
12.7	0.0	12.7	1.9
12.7	12.7	0.0	2.5
12.7	12.7	12.7	3.2

year, rainfall in the October–March period was 34% more than the 30-year mean; however, the age ratio at the Willow Springs check station was 2.9 JPA that same year. This observation added to total variability and reduced the predictive power of the neural model.

The pooled model (Freeman and Willow Springs data) with the outlier (6.7 juv/ad) removed explained 50% of the variation in age ratios ($P < 0.001$; Fig. 3). With the outlier removed, mean age ratios were 1.87 ± 1.02 JPA for the empirical data and 1.87 ± 0.73 JPA for the model predictions. The pooled model was used to explore the effects of rainfall and temperature patterns on production by Gambel's quail. With May–July temperatures held constant, the simulations indicated precipitation pattern affected relative production (Table 2). The neural model predictions indicated a gain of about 0.05–0.07 JPA/cm for precipitation in October–November and February–March; the estimated rate for December–January was about 0.09–0.11 JPA/cm. As was the case with call counts, rains in midwinter seemed to be more stimulating to production than rains in early or late winter.

The pooled age ratio model indicated variable effects of mean daily temperature on Gambel's quail production (Table 3). We held May temperatures constant at 23.9°C in this analysis. With July temperatures held constant, increasing temperatures in June within the range of 26.7–32.2°C had little effect on neural model predictions. When June temperatures were held constant, however, relative production declined at 0.18–0.25 JPA/°C within the range of 29.4–35.0°C in July.

Reproductive failure (<1 JPA) was associated with years subject to low rainfall from October to March and higher temperatures in July. The suppressing effect of low rainfall was moderated during cool years. For example, with no October–March rainfall, production was predicted to be 1.1 JPA in a cool year (23.9°C in May, 26.7°C in Jun, 29.4°C in Jul) compared to 0 JPA in a hot year (23.9°C in May, 32.2°C in Jun, 35.0°C in Jul).

The general pattern that emerged was a positive response to increasing precipitation and a

Table 3. Neural model predictions of age ratios (juv/ad) of Gambel's quail in response to mean daily temperatures in June and July and precipitation from October through March based on data collected in southcentral Arizona, 1978–96. Mean daily temperature in May was held constant at 23.9°C for these simulations.

Temperature (°C)		Precipitation (cm)[a] for each 2-month period during Oct–Mar		
June	July	0.0	6.3	12.7
26.7	29.4	1.1	2.6	3.9
	32.2	0.5	1.8	3.3
	35.0	0.0	1.1	2.6
29.4	29.4	1.0	2.5	3.9
	32.2	0.5	1.8	3.2
	35.0	0.0	1.1	2.5
32.2	29.4	1.0	2.5	3.8
	32.2	0.4	1.7	3.2
	35.0	0.0	1.0	2.5

[a] For example, the column 6.3 indicates 6.3 cm in Oct–Nov, Dec–Jan, and Feb–Mar.

negative response to increasing temperatures. Good production (1.5–3.0 JPA) could occur in years of moderate rainfall and cool temperatures or in years of high temperatures and profuse rainfall. High reproduction (>3.0 JPA) was associated with cooler years having higher rainfall.

DISCUSSION

To our knowledge, neural network modeling has received limited application in wildlife ecology (Recknagel et al. 1997, Maier et al. 1998, Olson and Cochran 1998), although it is used extensively in engineering and finance, among other applications (Kosko 1992, Anderson 1995, Smith 1996). Olson and Cochran (1998) recently reported neural net models explained more variation in tallgrass prairie biomass than multiple regression models. Backpropagation models such as we developed are subject to limitations (Anderson 1995:276–277), 2 of which are relevant to our work. First, there is a potential problem with overfitting the data such that generalization suffers. In other words, neural models can be constructed to fit training data perfectly, in which case the models may be of no value for general predictions. We addressed this problem by limiting the number of hidden nodes to ≤3 and testing the models with independent estimates of the dependent variables. Second, "a neural network may solve a practical problem, but it can be difficult to understand how it solved it" (Anderson 1995:277), meaning the process leading to neural predictions is not readily apparent from the construction and parameterization of the model. We can address this issue only by determining if model predictions are biologically reasonable and consistent with empirical results.

The neural predictions indicated that early winter rain (Oct–Nov) weakly affected calling behavior and age ratios. This prediction is plausible because the effect of rain in the warm, dry environment of Arizona rapidly wanes. The models predicted a relatively strong influence of mid- to late-winter rain, which is consistent with the findings of Swank and Gallizioli (1954). Also, highly variable calling intensity, as predicted (Table 1), is consistent with empirical estimates of 25–75% of males calling (Hungerford 1964).

High temperatures apparently do not limit the overall distribution of Gambel's quail (Gullion 1960), but Goldstein (1984) reported that Gambel's quail in the Colorado Desert exist near the upper lethal limit of thermal tolerance. During the summer, the thermal environment was the most important factor shaping the daytime activity budgets of Gambel's quail in his study area. Goldstein (1984) also noted that the thermal environment places greater constraints on young chicks because of their smaller body size.

We are not aware of any research on the effects of temperature on production by Gambel's quail. However, the suppressing effects of high temperatures during the nesting and brood-rearing season are documented for northern bobwhites (*Colinus virginianus*; Stanford 1972; Lehmann 1984:152–153; Forrester et al. 1998). High temperatures late in the production season reduce the length of the laying period for northern bobwhites (Klimstra and Roseberry 1975), which would reduce renesting activity. Guthery (1997) speculated that temperatures during the nesting season might be 1 of the major factors explaining variability in northern bobwhite production. Our findings on the interactive effects of rainfall and temperature are similar to those reported by Robinson and Baker (1955) for northern bobwhites in Kansas. Presumably, the same biophysical processes that associate higher temperatures with lower production in northern bobwhites could apply to Gambel's quail.

Predictions (call-count index, age ratios) of the neural models appear generally consistent with the empirical database on the relation between quail and weather variables (rainfall, temperature). The biological mechanisms that manifest these relations remain largely unknown and are fertile subjects for future research. In particular, more precise knowledge is needed on the factors leading to low reproductive rates during hot, dry years and high reproductive rates during cool, rainy years. These effects are assumed to be primarily nutrition based (e.g., Hungerford 1964), but temperature may make a significant contribution to variation in production. Heat is a physiological stressor that can inhibit laying hens, independent of nutrition. Negative effects of heat could manifest in the proportion of hens that lay (Guthery et al. 1988), staggered hatching within clutches (Stanford 1972), length of the laying season (Klimstra and Rosenberry 1975), and survival of chicks.

MANAGEMENT IMPLICATIONS

Our results provide several points of possible use in the management of Gambel's quail. We demonstrated that weather variables explain a large proportion of the variation in calling activity of males (i.e., calling frequency is to some extent independent of population size). Therefore, call counts may give misleading information on population status. Models that predict calling behavior based on weather variables could be used to standardize counts among years; Robel et al. (1969) showed how models may be used to standardize call counts of northern bobwhites.

Although rainfall and temperatures are beyond management control, nutrition and temperatures at quail level can be mediated through cover management (planting, grazing, brush management). Our results indicate management should attempt to foster cooler temperatures at quail level through the nesting and brood-rearing period. Finally, neural modeling of call counts and age ratios provides a method of understanding local variation in population behavior based on readily available weather records. Understanding this variation could assist state wildlife agencies in establishing harvest regulations, explaining population dynamics and providing interested publics with predictions of quail abundance.

ACKNOWLEDGMENTS

LITERATURE CITED

ANDERSON, J. A. 1995. An introduction to neural networks. MIT Press, Cambridge, Massachusetts, USA.

BOTTSFORD, L. W., AND J. G. BRITTNACHER. 1992. Detection of environmental influences on wildlife: the California quail as an example. Pages 158–169 *in* D. R. McCullough and R. H. Barrett,

editors. Wildlife 2001: populations. Elsevier Applied Science, New York, New York, USA.

BROWN, D. E. 1989. Arizona game birds. University of Arizona Press, Tucson, Arizona, USA.

———. 1994. Biotic communities: southwest United States and northwest Mexico. University of Utah Press, Salt Lake City, Utah, USA.

———, C. L. COCHRAN, T. E. WADDELL. 1978. Using call-counts to predict hunting success for scaled quail. Journal of Wildlife Management 42: 281–287.

CAMPBELL, H., D. K. MARTIN, P. E. FERKOVICH, AND B. K. HARRIS. 1973. Effects of hunting and some other environmental factors on scaled quail in New Mexico. Wildlife Monographs 34.

FORRESTER, N. D., F. S. GUTHERY, S. D. KOPP, AND W. E. COHEN. 1998. Operative temperature reduces habitat space for northern bobwhites. Journal of Wildlife Management 62:1506–1511.

FRANCIS, W. J. 1970. The influence of weather on population fluctuations in California quail. Journal of Wildlife Management 34:249–266.

GOLDSTEIN, D. L. 1984. The thermal environment and its constraint on activity of desert quail in summer. Auk 101:542–550.

GULLION, G. W. 1960. The ecology of Gambel's quail in Nevada and the arid Southwest. Ecology 41: 518–536.

GUTHERY, F. S. 1997. A philosophy of habitat management for northern bobwhites. Journal of Wildlife Management 61:291–301.

———, N. D. FORRESTER, K. R. NOLTE, W. E. COHEN, AND W. P. KUVLESKY, JR. 1999. Potential effects of global warming on quail populations. Proceedings of the National Bobwhite Quail Symposium 4:in press.

———, N. E. KOERTH, AND D. S. SMITH. 1988. Reproduction of northern bobwhites in semiarid environments. Journal of Wildlife Management 52: 144–149.

HAGAN, M. T., H. B. DEMUTH, AND M. BEALE. 1996. Neural network design. PWS-Kent Publishing, Boston, Massachusetts, USA.

HUNGERFORD, C. R. 1960. The factors affecting the breeding of Gambel's quail *Lophortyx gambelii* in Arizona. Dissertation, University of Arizona, Tucson, Arizona, USA.

———. 1964. Vitamin A and productivity in Gambel's quail. Journal of Wildlife Management 28:141–147.

KLIMSTRA, W. D., AND J. L. ROSEBERRY. 1975. Nesting ecology of the bobwhite in southern Illinois. Wildlife Monographs 41.

KOSKO, B. 1992. Neural networks and fuzzy systems. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

LEHMANN, V. W. 1953. Bobwhite population fluctuations and vitamin A. Transactions of the North American Wildlife Conference 18:199–246.

———. 1984. Bobwhites in the Rio Grande Plain of Texas. Texas A&M University Press, College Station, Texas, USA.

MAIER, H. R., G. C. DANDY, AND M. D. BURCH. 1998. Use of artificial neural networks for modeling cyanobacteria *Anabaena* spp. in the River

Murray, South Australia. Ecological Modelling 105:257–272.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINIS-TRATION. 1978–96. Climatological data annual summaries, Arizona. National Climatic Data Center, Asheville, North Carolina, USA.

OLSON, K. C., AND R. C. COCHRAN. 1998. Radiometry for predicting tallgrass prairie biomass using regression and neural models. Journal of Range Management 51:186–192.

RECKNAGEL, F., M. FRENCH, P. HARKONEN, AND K. I. YABUNAKA. 1997. Artificial neural network approach for modeling and predictions of algal blooms. Ecological Modelling 96:11–28.

ROBEL, R. J., D. J. DICK, AND G. F. KRAUSE. 1969. Regression coefficients used to adjust bobwhite quail whistle count data. Journal of Wildlife Management 33:662–668.

ROBINSON, T. S., AND R. H. BAKER. 1955. Climate and bobwhite quail in Kansas—1951–1954.

Transactions of the Kansas Academy of Science 58:353–359.

SMITH, M. 1996. Neural networks for statistical modeling. International Thompson Computer Press, New York, New York, USA.

SMITH, R. H., AND S. GALLIZIOLI. 1965. Predicting hunter success by means of a spring call count of Gambel quail. Journal of Wildlife Management 29:806–813.

STANFORD, J. A. 1972. Bobwhite quail population dynamics: relationships of weather, nesting, production patterns, fall population characteristics, and harvest in Missouri quail. Proceedings of the National Bobwhite Quail Symposium 1:115–139.

SWANK, W. G., AND S. GALLIZIOLI. 1954. The influence of hunting and of rainfall upon Gambel's quail populations. Transactions of the North American Wildlife Conference 19:283–297.