Research Article

Evidence for Regionally Synchronized Cycles in Texas Quail Population Dynamics

JEFFREY J. LUSK,[1,2] *Department of Forestry, Oklahoma State University, Stillwater, OK 74078, USA*
FRED S. GUTHERY, *Department of Forestry, Oklahoma State University, Stillwater, OK 74078, USA*
MARKUS J. PETERSON, *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA*
STEPHEN J. DEMASO, *Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, TX 78744, USA*

ABSTRACT Knowledge of the possible role of cyclic behavior in wildlife dynamics assists in understanding and managing populations. Using spectrum analysis, we analyzed time series (1978–2002) on the abundance of northern bobwhites (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) in several ecological regions in Texas, USA, to test for the presence of cycles; we also tested whether drought severity (Modified Palmer Drought Severity Index) exhibited cyclic dynamics and whether quail and drought cycles were synchronized among regions. We found evidence of population cyclicity in all ecoregions we tested (5 for bobwhites, 4 for scaled quail) based on both Texas Parks and Wildlife and North American Breeding Bird Survey count data. Periods of the observed cycles generally were 5–6 years (bobwhites) or 2–3 years (scaled quail), depending on ecoregion and data source. Cyclicity was most pronounced for bobwhites in the Rolling Plains (north TX) and the South Texas Plains. The Palmer Index exhibited a roughly 5-year cycle in 5 of 6 regions we tested. A 5-year bobwhite and Palmer Index cycle were synchronous in 3 contiguous ecoregions totaling 27,200,000 ha. Wet–dry cycles seemed to synchronize bobwhite cycles in Texas. Our results suggest that habitat manipulations aimed at improving habitat conditions during dry periods, such as reducing livestock stocking rates, could provide ground cover similar to that available in wet periods. (JOURNAL OF WILDLIFE MANAGEMENT 71(3):837–843; 2007)

DOI: 10.2193/2005-729

KEY WORDS *Callipepla squamata*, *Colinus virginianus*, cycles, northern bobwhites, Palmer Drought Severity Index, population dynamics, scaled quail, synchrony.

Cyclicity in wildlife dynamics has intrigued humankind since the sixteenth century, when "reliable men of great probity" observed Norwegian lemmings (*Lemmus* sp.) falling from the sky in large numbers on a 4-year cycle (Elton 1927:133). Cyclicity in North American grouse (Tetraonidae) has long been recognized (Leopold 1931, Schorger 1944, Darrow 1947). Northern bobwhites (*Colinus virginanus*) were early on considered noncyclic and the dynamic behavior of southwestern quail was unstudied (Leopold 1933). However, Errington (1945) conjectured that wild higher vertebrates of small to moderate size, including bobwhites, showed some semblance of 10-year periodicity in North America. Preno and Labisky (1971) noted, without formal analysis, an approximate 5-year cycle of bobwhites in Illinois, USA, based on calling-male surveys during 1956–1969.

Subsequently, cyclicity in quail dynamics has been assessed with greater quantitative rigor. Roseberry and Klimstra (1984) analyzed cyclicity in bobwhite dynamics in southern Illinois and identified an 8–10-year cycle that was coincident with the nodal cycle of the moon (Archibald 1977). In a more comprehensive examination of 73 time series largely on bobwhites in the eastern United States, 37 times series showed evidence of cyclicity with periods ranging from 4 to 17 years (Thogmartin et al. 2002). Excepting Williams (1963) and Thogmartin et al. (2002), who reported cycles for California quail (*Callipepla californicus*), we know of no analysis for species of New World quails other than bobwhites.

Proposed causes of population cycles are numerous and involve both intrinsic and extrinsic factors, although some form of density dependence seems necessary for cycles to develop in a population (May 1974, Kendall et al. 1999). Extrinsic factors proposed to explain cyclic trends include predator–prey and host–parasite interactions and environmental variation. Current theory holds that density-dependent factors are responsible for population cycles, whereas density-independent, extrinsic factors can alter the periodicity of the cycles and synchrony among spatially disjunct populations. The Moran effect (Moran 1953, Koenig 1999) has been proposed as such a density-independent, extrinsic mechanism leading to synchrony in population dynamics. Moran (1953) suggested that correlations in fluctuations among spatially disjunct populations (i.e., population synchrony) should equal correlations in environmental noise (e.g., weather) experienced by all populations, if the populations are regulated by the same density-dependent processes.

Annual variation in weather variables strongly influences quail dynamics, especially in semiarid environments. For example, the timing and quantity of precipitation affect the productivity of Montezuma quail (*Cyrtonyx montezumae*; Brown 1979), Gambel's quail (*Callipepla gambelii*; Swank and Gallizioli 1954), northern bobwhites (Kiel 1976), and scaled quail (*Callipepla squamata*; Campbell et al. 1973). Likewise, lower temperatures during a breeding season generally foster production, whereas higher temperatures tend to suppress it (Heffelfinger et al. 1999, Guthery et al. 2002). Thus, it is

[1] *E-mail: jeff.lusk@ngpc.ne.gov*
[2] *Present address: Nebraska Game & Parks Commission, 2200 N. 33rd Street, Lincoln, NE 68503, USA*

logical to examine the dynamics of weather variables in search of a possible influence on quail cycles, should such cycles exist. Further, because metapopulation persistence necessitates independent local-population dynamics (Harrison and Quinn 1989, Hanski 1999), whether populations exhibit synchrony is an important consideration for management and conservation of species in fragmented habitats.

We used bobwhite (5 ecoregions) and scaled quail (4 ecoregions) population indices in Texas, USA, during 1978–2002 to investigate evidence for cyclicity in quail dynamics. We further investigated the observed variability in periods (Thogmartin et al. 2002). We hypothesized that an observed period might be a sum of ≥ 2 embedded, periodic components, which might appear with different intensities in different data sets. Because quail abundance in Texas is correlated with weather variables (Bridges et al. 2001, Lusk et al. 2002), we examined whether a drought-severity index exhibited cyclic behavior and whether quail and weather cycles were synchronous over ecoregions during the period of record (1978–2002).

STUDY AREA

Data on quail dynamics were from annual roadside surveys conducted in August by the Texas Parks and Wildlife Department (TPWD; Peterson and Perez 2000, Peterson 2001) and from North American Breeding Bird Surveys conducted in May (BBS; Droege 1990). We analyzed data collected during 1978–2002 for the Gulf Prairies and Marshes, South Texas Plains, Edwards Plateau, Cross Timbers and Prairies, Rolling Plains, and Trans-Pecos ecoregions of Texas (Gould 1975). We analyzed bobwhite data for all regions except the Trans-Pecos (where few occur); scaled quail do not occur in the Gulf Prairies and Marshes or the Cross Timbers and Prairies (Anonymous 1945).

METHODS

Within each ecoregion, we calculated annual means for survey routes. We detrended the resulting means by first calculating an order-7 moving average (Kendall and Ord 1990) and then subtracting moving averages from the annual means to obtain residuals without temporal trend. An order-7 moving average was necessary to obtain a smooth curve sufficient for analysis. We further modified these residuals by removing the mean of the detrended data (i.e., $y_t - \bar{y}$ where $y_t =$ the detrended population index in yr t); this step was unnecessary but simplified presentation of results and standardized data for comparison among ecoregions and species.

We used spectrum analysis (Kendall and Ord 1990) to analyze the resulting data (detrended, $\bar{x}$ removed) for periodic behavior. Given that the mean is removed, under fairly general conditions a times series can be described as a Fourier series according to

$$y_t = \sum_{j=1}^{m} [a_j \cos(\alpha_j t) + b_j \sin(\alpha_j t)],$$

where

$$m = (n-1)/2 \text{ if } n \text{ is odd (our case)},$$

$$\alpha_j = 2\pi j/n, j = 1, 2, \cdots, m,$$

$$a_j = \frac{2}{n}\sum_{t=1}^{n} y_t \cos(\alpha_j t),$$

and

$$b_j = \frac{2}{n}\sum_{t=1}^{n} y_t \sin(\alpha_j t).$$

The complete series with $2m$ parameters will fit the transformed data perfectly ($r^2 = 1.0$), so a method is needed to assess the predictive contribution of a particular harmonic (value for j; the distance between peaks or troughs is n/j). Following Desportes et al. (1989), we determined the mean proportion of the variance explained by individual harmonics, calculated the upper 95% confidence level on that mean, and concluded a particular harmonic (i.e., embedded cycle) was significant if the proportion of variance explained exceeded the upper 95% confidence level on the mean. The lower 95% confidence level is not of interest (Desportes et al. 1989). To portray a time series using only the harmonics found to be significant, we simply added the appropriate sinusoids together. Our graphical results are sums of the 2 dominant sinusoids with dominance based on the proportion of the variance in the time series explained by a particular sinusoid.

We used the Modified Palmer Drought Severity Index as a composite weather variable because this index generally predicts quail abundance in Texas better than specific weather variables (Bridges et al. 2001). The index incorporates data on precipitation, temperature, and local soil conditions, among other variables. We obtained data for climatic regions of Texas from the National Climatic Data Center (Anonymous 2003). The climatic regions roughly coincide with Texas ecoregions (Bridges et al. 2001). For each region, we averaged monthly Palmer indices to obtain an index for a year and analyzed these yearly averages for periodicity in the same manner as for quail. We used the zero-lagged cross-correlation coefficient to assess the degree of synchrony between quail dynamics and the Palmer index (Bjørnstad et al. 1999, Koenig 1999, Schauber et al. 2002).

RESULTS

Cyclic components of dynamics explained from 42% of the variation in scaled quail dynamics in the Rolling Plains to 79% for bobwhite dynamics in the same ecoregion based on TPWD data (Table 1). For BBS data, cyclic components explained from 25% of the variation of scaled quail in the Rolling Plains to 53% for bobwhites in the Edwards Plateau (Table 2). We found evidence of cyclic behavior for both species in all ecoregions; according to the analysis, observed dynamics were based on the sum of 2 or 3 embedded cycles of different periods. We observed embedded cycles with

Table 1. Wavelength of component and pooled component cycles, along with proportion of variation in annual abundance explained for northern bobwhite and scaled quail dynamics in Texas, USA, ecoregions (Gould 1975) based on Texas Parks and Wildlife Department survey data, 1978–2002.

Species Ecoregion	Cycle wavelength (yr) Primary	Variation[a]	Secondary	Variation	Tertiary	Variation	Pooled	Variation
Northern bobwhite								
South Texas Plains	6.3	0.35	5.0	0.17			5.7	0.52
Gulf Prairies and Marshes	2.5	0.24	4.2	0.23	3.6	0.15	2.5	0.62
Edwards Plateau	12.5	0.34	5.0	0.17			5.5	0.51
Cross Timbers and Prairies	5.0	0.26	2.1	0.18			2.4	0.44
Rolling Plains	5.0	0.51	6.3	0.28			5.2	0.79
Scaled quail								
South Texas Plains	6.3	0.18	8.3	0.16	2.8	0.14	2.6	0.48
Edwards Plateau	12.5	0.28	2.1	0.20			2.1	0.48
Rolling Plains	5.0	0.25	4.2	0.17			4.5	0.42
Trans Pecos	2.1	0.17	2.8	0.14	3.1	0.12	2.5	0.43

[a] Proportion of variation in annual abundance explained by each periodic component.

2.3-, 2.5-, 2.8-, 3.1-, 3.6-, 4.2-, 5.0-, 6.3-, 8.3-, and 12.5-year periodicities. Periods of 4.2–6.3 years were most common in embedded cycles; quail of both species in all ecoregions—except for scaled quail in the Trans-Pecos and Edwards Plateau—exhibited cyclic behavior with 1 or 2 periods in this range. Sums of the cyclic components suggested periods of 2–3 (scaled quail) or 5–6 years (bobwhites), depending on ecoregion and data source (Tables 1, 2).

Graphical support (TWPD data) for cyclical dynamics was less compelling for some species–region combinations and more compelling for others. For example, scaled quail in the Rolling Plains exhibited cyclic behavior with roughly a 5-year period during 1978–1988 but subsequently the trajectory of the detrended population index was flat (Fig. 1). On the contrary, bobwhites in the South Texas Plains and Rolling Plains exhibited rather striking periodicity (Fig. 2).

For the Rolling and South Texas Plains, bobwhites had a 5-year cyclic component in both TPWD and BBS data (Tables 1, 2). Peaks in the BBS data tended to lag peaks in the TPWD data by 1–2 years in both ecoregions (Fig. 3).

A 5-year cycle was the dominant cycle for the Palmer Index in 4 of 6 ecoregions and it appeared as a secondary cycle in one ecoregion (Table 3). The sum of component cycles (pooled) revealed either 4–5- or 5–6-year cycles in 5 of 6 ecoregions. The predominant 5-year cycles for TPWD counts and the Palmer Index were in phase for the South Texas Plains, Edwards Plateau, and Rolling Plains (Fig. 4). These contiguous regions total 27,200,000 ha in Texas (Gould 1975). Zero-lagged cross-correlations supported these results for the TPWD data, indicating significant correlations between bobwhite counts and the Palmer Index in 4 of 5 ecoregions (Table 4).

The results generally were supportive of a 4–6-year cycle in quail and weather dynamics in Texas. For northern bobwhites, a 5-year cycle appeared in 4 of 5 tests based on TPWD data (Table 1) and 5 of 5 tests based on BBS (Table 2) and Palmer Index data (Table 3; 14 of 15 tests positive for 5-yr cycle). A 5-year cycle also appeared for scaled quail with BBS (Table 2) and Palmer Index data in the Trans-Pecos (Table 3). However, the pattern of scaled quail cyclicity was somewhat ambiguous relative to bobwhites. The cross-correlation analysis indicated that scaled quail counts were synchronous with the Palmer Index only in the Trans Pecos (Table 4).

DISCUSSION

An assumption in our analysis was that the indices of abundance (TPWD, BBS) were approximately zero-inter-

Table 2. Wavelength of component and pooled component cycles, and proportion of variation explained for northern bobwhite and scaled quail dynamics in Texas, USA, ecoregions (Gould 1975) based on North American Breeding Bird Surveys, 1978–2002.

Species Ecoregion	Cycle wavelength (yr) Primary	Variation[a]	Secondary	Variation	Tertiary	Variation	Pooled	Variation
Northern bobwhite								
South Texas Plains	5.0	0.17	8.3	0.15	2.5	0.12	5–6	0.44
Gulf Prairies & Marshes	5.0	0.28	12.5	0.13			5–6	0.41
Edwards Plateau	12.5	0.36	5.0	0.17			5–6	0.53
Cross Timbers & Prairies	12.5	0.23	5.0	0.22			5–6	0.45
Rolling Plains	5.0	0.21	2.5	0.16	6.3	0.15	5–6	0.52
Scaled quail								
South Texas Plains	2.8	0.27	2.5	0.22			2–3	0.49
Rolling Plains	8.3	0.25					8–9	0.25
Trans-Pecos	4.2	0.19	5.0	0.16	2.3	0.14	2–3	0.49

[a] Proportion of variation in annual abundance explained by each periodic component.

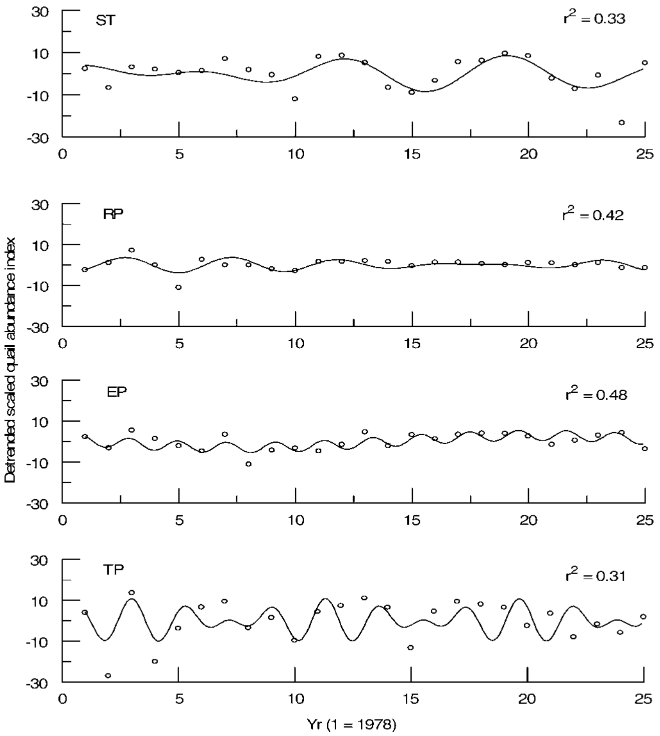

Figure 1. Cyclic components of dynamics for scaled quail in Texas, USA, ecoregions based on Texas Parks and Wildlife Department counts, 1978–2002. Ecoregions (Gould 1975) were ST = South Texas Plains, RP = Rolling Plains, EP = Edwards Plateau, and TP = Trans-Pecos.

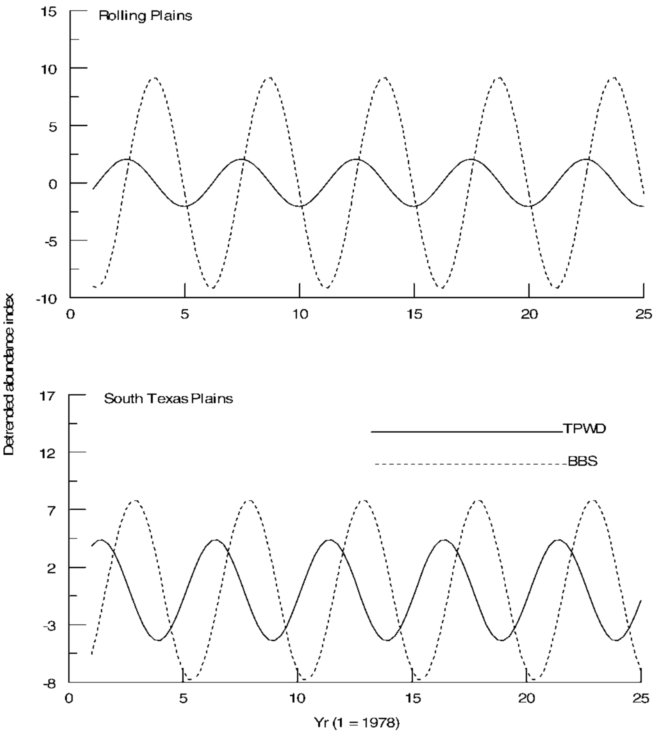

Figure 3. Comparative 5-year cycles of northern bobwhites in the Rolling and South Texas Plains, USA, based on Texas Parks and Wildlife Department (TPWD) and North American Breeding Bird Survey (BBS) data, 1978–2002.

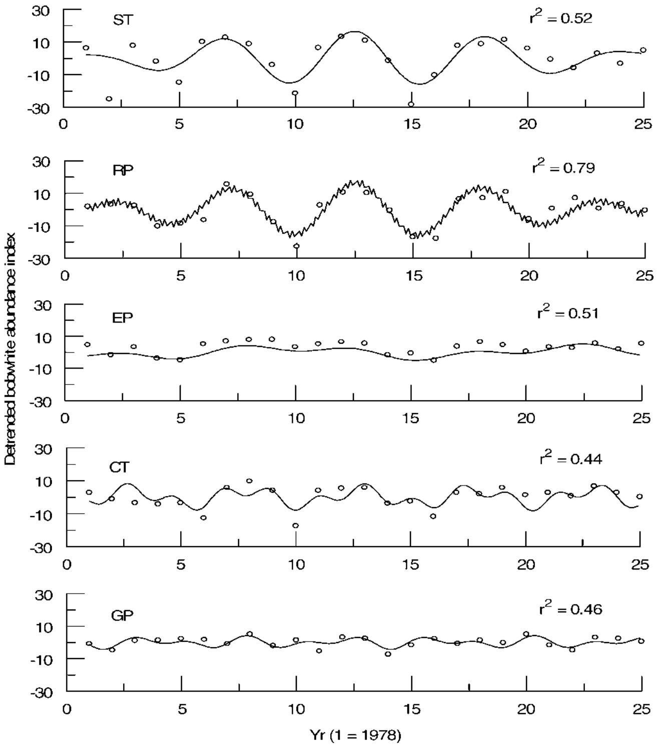

Figure 2. Cyclic components of dynamics for northern bobwhites in Texas, USA, ecoregions based on Texas Parks and Wildlife Department counts, 1978–2002. Ecoregions (Gould 1975) were ST = South Texas Plains, RP = Rolling Plains, EP = Edwards Plateau, CT = Cross Timbers and Prairies, and GP = Gulf Prairies and Marshes.

cept, linear functions of population abundance. Lusk et al. (2002) suspected that TPWD data were biased high during hot summers. On the other hand, the assumption has support because at local scales hunting success may be expressed as a linear function of quail abundance (Brown et al. 1978, Guthery 1986, Palmer et al. 2002) and at state scales total harvest may be expressed as a linear function of the TPWD index (Peterson and Perez 2000, DeMaso et al. 2002, Guthery et al. 2004). These findings imply a linear relation between population size and the abundance index. The zero-intercept condition is tenable because an abundance index would be zero if the quail population was zero. Thus, evidence suggests that although bias may have been present in the TPWD index, the index probably was correlated with population abundance. We assume similar arguments held for the BBS data.

We found evidence for cycles among populations of bobwhites with periods between 5 and 6 years coincident with a 5-year cycle in the Palmer Index, which resulted in synchrony among ecoregions. These results add to the literature on population cycles and synchrony among gallinaceous species (e.g., Hudson et al. 1998, Cattadori and Hudson 1999, Cattadori et al. 1999). A potential cause of cyclic dynamics in quail is delayed density dependence interacting with environmental perturbations (Thogmartin et al. 2002). Environmental perturbations could include drought throughout Texas and occasional severe winters in the Rolling Plains. Bobwhite populations in the South Texas and Rolling Plains fluctuated markedly during 1978–

Table 3. Wavelength of component and pooled component cycles of dynamics and the proportion of variation in drought index explained for the Modified Palmer Drought Severity Index for the National Oceanic and Atmospheric Administration climatic regions of Texas, USA, 1978–2002.

	Cycle wavelength (yr)							
Climate region—ecoregion	Primary	Variation[a]	Secondary	Variation[a]	Tertiary	Variation	Pooled	Variation
9—South Texas Plains	5.0	3.9	2.1	0.13			4–5	0.42
8—Gulf Prairies & Marshes	12.5	0.35	5.0	0.13			5–6	0.48
6—Edwards Plateau	5.0	0.38	2.3	0.17			4–5	0.55
3—Cross Timbers & Prairies	12.5	0.23	2.5	0.16	3.1	0.15	2	0.54
2—Rolling Plains	5.0	0.24	2.5	0.17			5	0.41
5—Trans-Pecos	5.0	0.21	6.3	0.19	2.3	0.17	4–5	0.57

[a] Proportion of variation in drought index explained by each periodic component.

1999 but exhibited no temporal trend in abundance based on TPWD count data (DeMaso et al. 2002). Likewise, scaled quail exhibited no temporal trend in abundance in the South Texas Plains during this period. On the contrary, bobwhites and scaled quail populations declined during 1978–1999 in all other ecoregions. These declines were associated with a reduction in variability of the detrended population index (Figs. 1, 2). The declines also could have removed or suppressed density-dependent population behavior (i.e., populations at low levels might not have expressed observable density-dependent behavior because the birds were too few for density-dependent responses to occur).

Another explanation for cyclic behavior in Texas bobwhite populations was the cyclic behavior in the Palmer Modified Drought Severity Index. This index, though called a drought index, also could be called a wetness index. Index values <0 indicate drought, near zero indicate normal conditions, and >0 indicate rainy periods. We found significant synchrony between the Palmer Index and the TPWD bobwhite counts (Table 4). To function as a driver of cyclic population dynamics, a factor should alter the demographic parameters of a population. Biologically, drought and high temperatures reduce length of the laying season (Klimstra and Roseberry 1975), the percentage of hens laying, and the total reproductive effort in a breeding season (Guthery et al. 1988). Rainy periods reverse the effects of drought on these demographic variables. If quail populations encounter dry and wet periods that arrive in a periodic manner, it seems the populations would respond with cyclic dynamics. Although these weather effects are density independent, we do not deny the role of density-dependent processes in driving the cycles we detected in our time series. It is possible that weather factors underlying the Palmer Index alter aspects of the habitat resulting in changes in the carrying capacity, resulting in density-dependent population regulation.

We acknowledge that any "time series may be decomposed into a set of cycles based on the harmonic frequencies. This does *not* mean that the phenomenon under study displays cyclical behaviour" (Kendall and Ord 1990:158; emphasis in original). Accordingly, we view our results with skepticism. We conducted the equivalent of 276 statistical

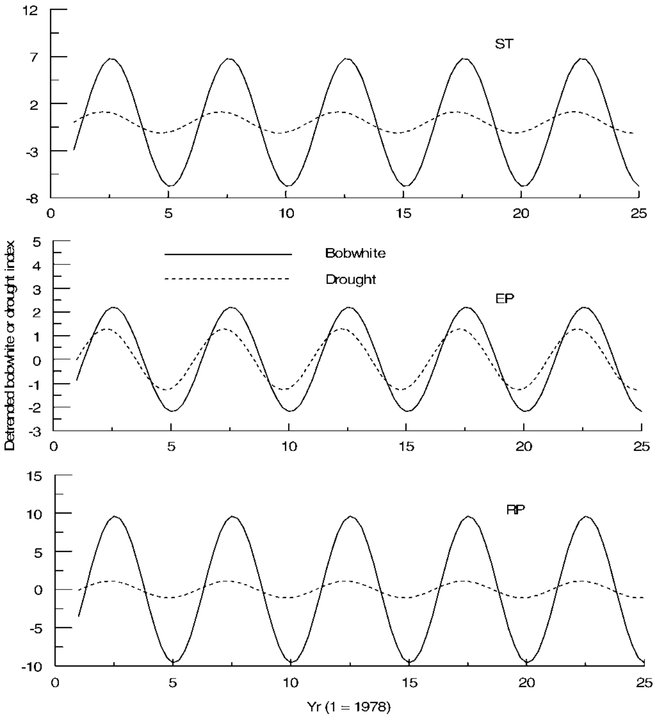

Figure 4. Regional synchronization of 5-year cycles of northern bobwhites based on Texas Parks and Wildlife data and the Modified Palmer Drought Severity Index in 3 Texas, USA, ecoregions, 1978–2002. Ecoregions (Gould 1975) were ST = South Texas Plains, EP = Edwards Plateau, and RP = Rolling Plains.

Table 4. Zero-lagged cross-correlation coefficients (r_p) *P*-values, and 95% confidence intervals for analysis of the synchrony between Texas Parks and Wildlife Department counts and the Modified Palmer Drought Severity Index for the National Oceanic and Atmospheric Administration climatic regions of Texas, USA, 1978–2002.

Climate region—ecoregion	Species	r_p	*P*	95% CI
9—South Texas Plains	Bobwhite	0.50	0.013	0.12–0.75
	Scaled	0.21	0.335	−0.22–0.56
8—Prairie Gulf & Marshes	Bobwhite	0.05	0.801	−0.36–0.45
6—Edwards Plateau	Bobwhite	0.46	0.025	0.07–0.73
	Scaled	0.18	0.394	−0.24–0.55
3—Cross Timbers & Prairies	Bobwhite	0.37	0.074	−0.04–0.67
2—Rolling Plains	Bobwhite	0.61	0.002	0.27–0.81
	Scaled	0.07	0.748	−0.34–0.46
5—Trans Pecos	Scaled	0.47	0.022	0.08–0.73

tests and we would expect 14 significant results at the 95% confidence level, more if, as in our case, there was autocorrelation (i.e., synchrony) observed. We found 46 significant cycles, indicating apparent substance to the population behavior. Moreover, for bobwhites in the South Texas Plains, Edwards Plateau, and Rolling Plains, 5-year periodicities were in-phase for TPWD counts and Palmer drought data (Fig. 4) in 27,200,000 ha. This observed synchrony was significant as indicated by the zero-lagged cross-correlation analysis (Table 4). The high prevalence of a 5-year cycle for bobwhites and drought data (Tables 1, 2, 3) also lends credence to a cyclic pattern for the birds in Texas. We attribute the observation that BBS and TPWD data were asynchronous to the fact that BBS surveys were conducted in May, before reproduction, and TPWD surveys in August, after most reproduction in a given year. The pulse in production might not appear in BBS data until a succeeding year. Also, evidence of cyclicity in Texas bobwhites previously has been reported (Thogmartin et al. 2002). These authors identified what they termed a quasi-cycle (an apparent cycle that was not significant at $P < 0.05$) with a period of 6–7 years based on BBS data. Their analysis was based on lagged correlations in the abundance index, which differed from our spectrum approach.

To the extent that our analyses reflected biological reality, populations of bobwhites and scaled quail in Texas may experience periodic rhythms of different wavelengths embedded in an observed cycle of fixed wavelength. For example, scaled quail in the Edwards Plateau seemed to have 2.1- and 12.5-year cycles embedded in what manifested as a 2.1-year cycle (sum of cyclic waves; Table 1). This raises the possibility that the variability in period length observed by Thogmartin et al. (2002) was due in part to embedded cycles that manifested at different intensities in different datasets. Our analysis demonstrated the possibility of embedded cycles, the existence of which can be confirmed or refuted with further time-series analyses and better understanding of the causative mechanisms that induce cyclic behavior in quail populations.

Our results suggested that bobwhite cycles are synchronized over a vast geographical area in Texas, indicating that population dynamics were likely synchronous over the same area. Some evidence points to the role of environmental cues, such as weather factors (e.g., Ranta et al. 1995, Lindström et al. 1996, Watson et al. 2000), in synchronizing spatially disparate populations. Whereas cycles are largely the result of density-dependent factors, the synchrony of these cyclic fluctuations among populations is governed by extrinsic environmental conditions: "[l]ocal populations (belonging to one or more species) with similar density dependence structures will become synchronized under the perturbation of density-independent factors, if the factors are correlated between regions" (Ranta et al. 1995:774). Cattadori et al. (1999) investigated the synchrony of cyclic dynamics for rock partridge in the Italian Alps. They found that populations in dry habitats tended to cycle more than populations in wet habitats, with a period of 4–7 years, and populations within similar habitats were synchronous. This implies that there was an overarching environmental influence operating on these populations, but that populations among different habitat types were governed by different density-dependent processes resulting in asynchrony (Cattadori et al. 1999).

Our results have implications with respect to harvest and habitat management. Our results suggest a density-independent component of quail dynamics in Texas, which does not preclude a density-dependent component also acting on quail dynamics. The density-independent component implies additivity in harvest mortality. For example, Williams et al. (2004) observed density-independent survival associated with fully additive harvest of bobwhites in Kansas. Of course, strength of additivity must be coupled to harvest rate to determine harvest impacts on quail populations.

MANAGEMENT IMPLICATIONS

With respect to habitat management, our results suggested rhythmic pulses in the nature of habitat associated with like pulses in wet and dry periods. Management cannot alter the weather, so random or cyclic variation in quail populations is to some degree beyond management control. However, the nature of habitat during wet periods provides a conceptual goal in habitat management during dry periods. On Texas rangeland, which comprises the bulk of the Trans-Pecos, South Texas Plains, Edwards Plateau, and Rolling Plains, lowered livestock stocking rates during dry periods likely would foster ground cover more similar to that available during wet periods. There is a general tendency for bobwhite abundance to decline with increased stocking rate in Texas (Lusk et al. 2002).

ACKNOWLEDGMENTS

We thank W. D. Koenig, J. Cooke, and 2 anonymous reviewers for commenting on drafts of the manuscript. The Bollenbach Endowment, Game Bird Research Fund, Department of Forestry, and Oklahoma Agricultural Experiment Station supported work by Guthery and Lusk. The Texas Agricultural Experiment Station and Texas A&M University supported Peterson's contributions. Lusk was supported during preparation of the manuscript by the Department of Forestry and Natural Resources at Purdue University. We acknowledge support from the Texas Parks and Wildlife Department (Federal Aid Project W-126-R-11). This manuscript was approved for publication by the Oklahoma and Texas Agricultural Experiment Stations.

LITERATURE CITED

Anonymous. 1945. Principal game birds and mammals of Texas. Texas Game, Fish and Oyster Commission, Austin, USA.

Anonymous. 2003. National Climate Data Center. <http://www.ncdc.noaa.gov/oa/climate/research/drought/palmer-maps/>. Accessed 3 Mar 2007.

Archibald, H. L. 1977. Is the 10-year wildlife cycle induced by a lunar cycle? Wildlife Society Bulletin 5:126–129.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution 14:427–432.

Bridges, A. S., M. J. Peterson, N. J. Silvy, F. E. Smeins, and X. B. Wu. 2001. Differential influence of weather on regional quail abundance in Texas. Journal of Wildlife Management 65:10–18.

Brown, D. E. 1979. Factors influencing reproductive success and population densities of Montezuma quail. Journal of Wildlife Management 43:522–526.

Brown, D. E., C. L. Cochran, and T. E. Waddell. 1978. Using call-counts to predict hunting success for scaled quail. Journal of Wildlife Management 42:281–187.

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.

Cattadori, I. M., and P. J. Hudson. 1999. Temporal dynamics of grouse populations at the southern edge of their distribution. Ecography 22:374–383.

Cattadori, I. M., P. J. Hudosn, S. Merler, and A. Rizzoli. 1999. Synchrony, scale and temporal dynamics of rock partridge (*Alectoris graeca saxatilis*) populations in the Dolmites. Journal of Animal Ecology 68:540–549.

Darrow, R. W. 1947. Fluctuations in grouse abundance. Pages 555–579 *in* G. Bump, R. W. Darrow, F. C. Edminster, and W. F. Crissey, editors. The ruffed grouse: life history, propagation, and management. State of New York Conservation Department, Albany, USA.

DeMaso, S. J., M. J. Peterson, J. R. Purvis, N. J. Silvy, and J. L. Cooke. 2002. A comparison of two quail abundance indices and their relationship to quail harvest in Texas. Proceedings of the National Quail Symposium 5:206–212.

Desportes, J.-P., N. B. Metcalfe, F. Cezilly, G. Lauvergeon, and C. Kervella. 1989. Tests of the sequential randomness of vigilant behaviour using spectral analysis. Animal Behavior 38:771–777.

Droege, S. 1990. The North American Breeding Bird Survey. Pages 1–4 *in* J. R. Sauer and S. Droege, editors. Survey designs and statistical methods for estimation of avian population trends. U.S. Fish and Wildlife Service Biological Report 10, Washington, D.C., USA.

Elton, C. 1927. Animal ecology. Sidgwick & Jackson, London, United Kingdom.

Errington, P. L. 1945. Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena. Ecological Monographs 15:1–34.

Gould, F. W. 1975. Texas plants: a checklist and ecological summary. Texas Agricultural Experiment Station Miscellaneous Publication 585, College Station, USA.

Guthery, F. S. 1986. Beef, brush and bobwhites. Ceasar Kleberg Wildlife Research Institute Press, Kingsville, Texas, USA.

Guthery, F. S., A. K. Crews, J. J. Lusk, R. N. Chapman, and M. Sams. 2004. Effects of bag limits on bobwhite hunters and harvest. Journal of Wildlife Management 68:1095–1103.

Guthery, F. S., N. E. Koerth, and D. S. Smith. 1988. Reproduction of northern bobwhites in semiarid environments. Journal of Wildlife Management 52:144–149.

Guthery, F. S., J. J. Lusk, D. R. Synatzske, J. Gallagher, S. J. DeMaso, R. R. George, and M. J. Peterson. 2002. Weather and age rations of northern bobwhites in South Texas. Proceedings of the National Quail Symposium 5:99–105.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, United Kingdom.

Harrison, S., and J. F. Quinn. 1989. Correlated environments and the persistence of metapopulations. Oikos 56:293–298.

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

Hudson, P. J., A. P. Dobson, and D. Newborn. 1998. Prevention of population cycles by parasite removal. Science 282:2256–2258.

Kendall, B. E., C. J. Briggs, W. W. Murdoch, P. Turchin, S. P. Ellner, E. McCauley, R. M. Nisbet, and S. N. Wood. 1999. Why do populations cycle? A synthesis of statistical and mechanistic approaches. Ecology 80: 1789–1805.

Kendall, S. M., and K. Ord. 1990. Time series. Oxford University Press, United Kingdom.

Kiel, W. H. 1976. Bobwhite quail population characteristics and management implications in South Texas. Transactions of the North American Wildlife and Natural Resources Conference 41:407–420.

Klimstra, W. D., and J. L. Roseberry. 1975. Nesting ecology of the bobwhite in southern Illinois. Wildlife Monographs 41.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology and Evolution 12:22–26.

Leopold, A. 1931. Report on a game survey of the north central states. Democrat, Madison, Wisconsin, USA.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York, New York, USA.

Lindström, J., E. Ranta, and H. Lindén. 1996. Large-scale synchrony in the dynamics of capercaillie, black grouse, and hazel grouse populations in Finland. Oikos 76:221–227.

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.

May, R. M. 1974. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. Science 186:645–647.

Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle: II. Synchrony and meteorology. Australian Journal of Zoology 1:291–298.

Palmer, W. E., S. D. Wellendorf, L. A. Brennan, W. R. Davidson, and F. E. Kellogg. 2002. Hunting success and northern bobwhite density on Tall Timbers Research Station: 1970–2001. Proceedings of the National Quail Symposium 5:213–216.

Peterson, M. J. 2001. Northern bobwhite and scaled quail abundance and hunting regulation: a Texas example. Journal of Wildlife Management 64:828–837.

Peterson, M. J., and R. M. Perez. 2000. Is quail hunting self regulatory?: northern bobwhite and scaled quail abundance and quail hunting in Texas. Proceedings of the National Quail Symposium 4:85–91.

Preno, W. L., and R. F. Labisky. 1971. Abundance and harvest of doves, pheasants, bobwhites, squirrels, and cottontails in Illinois, 1956–69. Illinois Department of Conservation Technical Bulletin 4, Springfield, USA.

Ranta, E., J. Lindström, and H. Lindén. 1995. Synchrony in tetraonid population dynamics. Journal of Animal Ecology 64:767–776.

Roseberry, J. L., and W. D. Klimstra. 1984. Population ecology of the bobwhite. Southern Illinois University Press, Carbondale, USA.

Schauber, E. M., D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan, and R. E. Brockie. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. Ecology 83:1214–1225.

Schorger, A. W. 1944. The prairie chicken and sharp-tailed grouse in early Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 36:1–59.

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.

Thogmartin, W. E., J. L. Roseberry, and A. Woolf. 2002. Cyclicity in northern bobwhites: a time-analytic review of the evidence. Proceedings of the National Quail Symposium 5:192–200.

Watson, A., R. Moss, and P. Rothery. 2000. Weather and synchrony in 10-year population cycles of rock ptarmigan and red grouse in Scotland. Ecology 81:2126–2136.

Williams, C. K., R. S. Lutz, and R. D. Applegate. 2004. Winter survival and additive harvest in northern bobwhite coveys in Kansas. Journal of Wildlife Management 68:94–100.

Williams, G. R. 1963. A four-year population cycle in California quail, *Lophortyx californicus* (Shaw) in the south island of New Zealand. Journal of Animal Ecology 32:441–459.

Associate Editor: Brennan.