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CYCLICITY IN NORTHERN BOBWHITES: A TIME-ANALYTIC REVIEW OF THE EVIDENCE

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ABSTRACT

Cyclical behavior in wildlife populations, including northern bobwhite (*Colinus virginianus*), has long fascinated human observers. However, studies examining cyclicity of bobwhite abundance have yielded contradictory results. We reviewed evidence for periodic fluctuation in bobwhite abundance by studying 73 long-term time series. Our aim was to discern with time-series techniques whether cyclicity occurred in bobwhite abundance. We elucidated the frequency of occurrence, geographical distribution, and potential mechanisms responsible for cyclicity. Approximately one-half ($n = 37$) of the populations examined demonstrated cyclical behavior, with a period varying between 4 and 17 yrs. True cycles, consistent, significant fluctuations in abundance, were rare, occurring in only 3 time series. The predominant form of periodicity was of the phase-forgetting quasi-cycle type ($n = 34$). This phase-forgetting may have contributed to previous contradictory findings of cyclicity in this species. We reason cyclicity in bobwhite populations is caused by aperiodic environmental perturbations interacting with density-dependence. Cyclic bobwhite populations occupied the northern and western portion of the species' range, where stochastic weather events regularly negatively influence bobwhite population dynamics. Bobwhite populations were non-cyclic in the relatively consistent climate of the southeastern United States, however, habitat fragmentation rather than climate may have contributed to the absence of cyclicity in this region.

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Key words: California quail, *Callipepla californica*, *Colinus virginianus*, density dependence, environmental forcing, northern bobwhite, periodicity, phase-forgetting quasi-cycles

INTRODUCTION

Northern bobwhite abundance is highly variable between years over much of the species' range (Stoddard 1931:339–347, Rosene 1969:194–197, Schwartz 1974, Peterson and Perez 2000), with populations fluctuating as much as 70% or more around the long-term mean (Roseberry and Klimstra 1984:122). Throughout much of the quail range these fluctuations appear primarily due to differences in overwinter mortality (Scott 1937, Mosby and Overton 1950, Kozicky and Hendrickson 1952, Kabat and Thompson 1963, Stanford 1972) and subsequent reproductive success (Parmalee 1955, Robinson 1957, Speake and Haugen 1960, Schemnitz 1964, Lehmann 1984, Forrester et al. 1998).

Roseberry and Klimstra (1984) suggested the increasing phase in bobwhite population fluctuations was generally gradual and steady in their southern Illinois study of bobwhite population dynamics. Declines, however, took 1 of 2 paths, either tumbling sharply in 1 year or declining at a rate similar to the increases occurring over a span of 3–4 years. Williams (1963)

found similar results for California quail (*Callipepla californica*). Such gradual change is indicative of serial correlation (temporal autocorrelation) in abundance.

Roseberry and Klimstra (1984:151–191) indicated these correlated fluctuations contributed to cyclic patterns in abundance. A cycle may be defined as a fluctuation having period, timing, and amplitude (Wing 1955). Mathematically, for animals to cycle, a time series $\{y(t)\}$ is periodic if there exists a period of length T such that:

$$y(t + T) = y(t)$$

(Lindström et al. 1997). Unlike the 10-year cycles of northern grouse (Tetraonidae; Keith 1963), Preno and Labisky (1971) believed bobwhites cycled on a 5-year basis ($T = 5$), whereas Roseberry and Klimstra (1984) thought it was 8–10 yrs. Wing (1955) believed bobwhites cycled on ~4-year period (either 3.8, 4.2, or 4.4 yrs), as did Williams (1963) for California quail ($T = 4$). Other authors reported no evidence of cyclicity in their study population (e.g., Errington 1957, Brennan et al. 2000).

NORTHERN BOBWHITE CYCLICITY

193

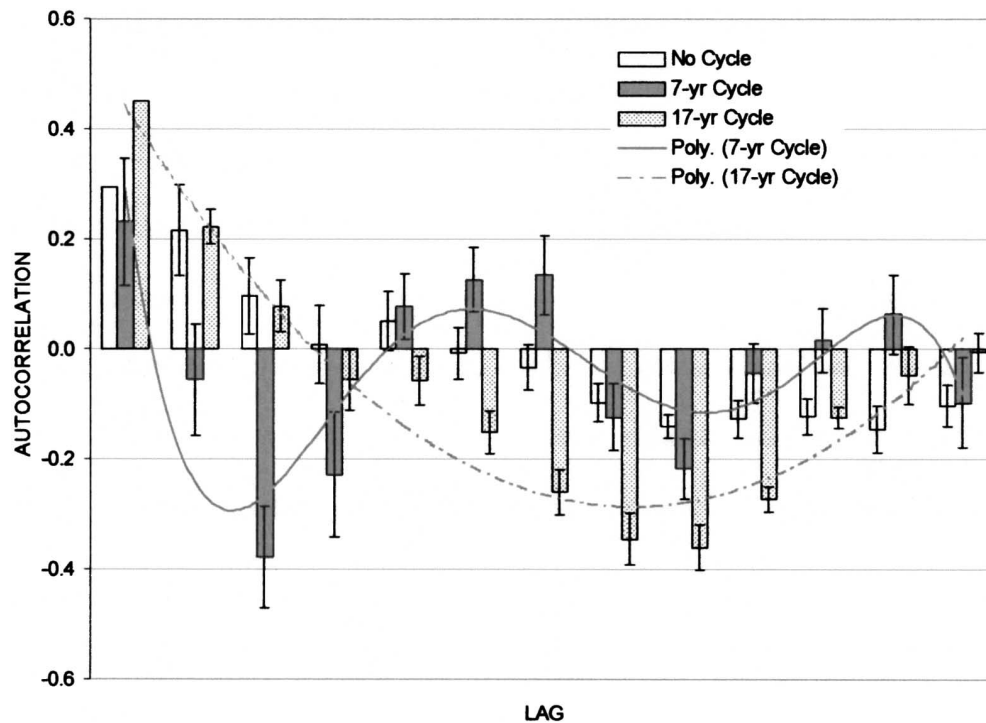


Fig. 1. Autocorrelation functions for 7-year cycle, 17-year cycle, and non-cyclic northern bobwhite populations in Illinois, as determined by route-level counts from the North American Breeding Bird Survey. Autocorrelation function significant at $r = 0.346$; correlations at lags ≥ 8 are tentative due to decreased sample size.

Recognizing patterns in population abundance is a precondition for uncovering mechanisms responsible for producing them (Lindström et al. 1997) and, as Edwards (1972) suggested, if wildlife managers can begin to predict these fluctuations (i.e., their direction and strength) management actions will be more effective. For instance, if the cyclic aspect of a population's dynamics suggest a downward turn in the population in the near future, management will not needlessly over-react knowing that a natural upturn will follow shortly thereafter.

We examined whether temporal patterns of variability in bobwhite abundance in Illinois were periodic. In addition, we reviewed published data testing cyclicity in bobwhites, as well as other long-term data sets amenable to analysis. Our purpose was to elucidate the frequency of occurrence, geographical distribution, and potential mechanisms responsible for cyclicity.

METHODS

Time series analysis follows 2 general approaches (Box and Jenkins 1970). One approach, the frequency domain, examines dominant periodicities or cyclical patterns in a time series. Conversely, time-domain analysis examines the structural pattern of a time series, analyzing the values of a process directly. Combining both approaches is often useful in gleaning a better understanding of the data series. While we conducted frequency-domain analyses (e.g., spectral analysis), we confined final analyses to the time domain

due to the subjective nature of period determination by frequency-domain analyses coupled with the shortness of many time series.

We examined several sources of long-term abundance data. We examined route- and state-summarized North American Breeding Bird Survey (NABBS) data for Illinois. These data were available for 26 routes, for 1967–1998 ($n = 32$ years), primarily through the west-central and southern portions of the state. We also (re-) examined cyclicity in data provided by Wing (1937:326; $n = 19$ and 24 yrs), Errington (1957:289; $n = 18$ and 18 yrs), Kabat and Thompson (1963:21; $n = 23$ and 25 yrs), Williams (1963; $n = 12, 13,$ and 13 yrs), Rosene (1969:381; $n = 10$ yrs), Mitchell (1979:11; $n = 34$ yrs), Roseberry and Klimstra (1984:73; $n = 26$ and 26 yrs), and Brennan et al. (2000; $n = 39, 53,$ and 91 yrs). The Kabat and Thompson (1963) data set contained Errington's data, plus an additional 4 years of spring and 8 years of autumn counts. The Williams (1963) data were counts of California quail introduced to New Zealand. We also examined Illinois fall harvest ($n = 24$ yrs) and Christmas Bird Counts ($n = 41$ yrs) for evidence of periodicity. The third data set examined was annual NABBS counts from 29 eastern states (not including Ill.; 1967 or 1968–2000, range = 33–34 yrs). In total, we examined 73 time series of varying length (range = 10–91 yrs), occurring throughout the species range. Since population dynamics relate to multiplicative processes (Williamson 1971), all abundance indices were log-transformed ($\log[\text{ABUNDANCE} + 1]$) to stabilize variances (Sen and Srivastava 1990).

Table 1. Cyclic patterns in quail. *T* is period of cycle, PFQC is phase-forgetting quasi-cycle.

Data Set	Location	Type	Season	Time Series Length	<i>T</i>	Cyclic Pattern
Wing (1937)	Oh.	Census	Winter	1908–1931	14?	PFQC
Wing (1937)	Pa.	unknown ^a	unknown ^a	1915–1933	14?	PFQC
Errington (1957)	Wis.	Census	Spring	1930–1947	8	PFQC
Errington (1957)	Wis.	Census	Autumn	1929–1946	8–9	PFQC
Kabat and Thompson (1963)	Wis.	Census	Spring	1929–1951	8	PFQC
Kabat and Thompson (1963)	Wis.	Census	Autumn	1929–1955	8	PFQC
Rosene (1969)	S.C.	Census	Autumn ^b	1957–1967	5	PFQC
Mitchell (1979)	Neb.	Mail-Carrier	Summer	1945–1978		Noncyclic
Roseberry and Klimstra (1984)	Ill.	Census	Spring	1954–1979	8–9	PFQC
Roseberry and Klimstra (1984)	Ill.	Census	Autumn	1954–1979	8	Definitely Cyclic
Brennan et al. (2000)	Ga.	Coveys Flushed, Plantation "C"	Autumn	1960–1997		Noncyclic
Brennan et al. (2000)	Ga.	Coveys Flushed, Plantation "D"	Autumn	1938–1990		Noncyclic
Brennan et al. (2000)	Ga.	Coveys Flushed, Plantation "E"	Autumn	1906–1996		Noncyclic
Harvest	Ill.	Harvest	Autumn/Winter	1975–1998		Noncyclic
Christmas Bird Counts	Ill.	Counts	Winter	1967–2000		Noncyclic

^a Author did not indicate season or census type.

^b Estimate made at start of hunting season, in fall.

For NABBS time series of routes with gaps in the data, we averaged the neighboring data values when the gap was 1 year. Time series with gaps ≥ 2 years were excluded. Routes were also excluded when the time series possessed ≥ 3 , 1-year gaps or ≥ 3 years with zero counts. To insure a lengthy period for analysis, only routes extending ≥ 20 years were included. Because we were interested in periodic fluctuations within time-series, we removed long-term trends by fitting 1st- and 2nd-order polynomial and LOESS regressions. The method for removing the long term trend is vital and we were conservative in our application, always choosing the less aggressive option (i.e., erring on the side of non-stationarity rather than removing too much variation due to trend).

Detection of temporal autocorrelation for each time series (i.e., correlation within a single time series) was accomplished with lagged scatter plots, autocorrelation function (ACF) plots, and partial autocorrelation function (PACF) plots (Brockwell and Davis 1987). Cyclicity of the time series was assessed by identifying recurring peaks and valleys in the ACFs. Evidence for true cyclicity occurred when multiple lags exceeded Bartlett’s line, a significance level derived from convergence of sample correlation coefficients to the normal distribution (Lindström et al. 1997). Weaker evidence for cyclicity (Nisbet and Gurney 1982), was suggested when recurring patterns were observed but the lagged autocorrelations were

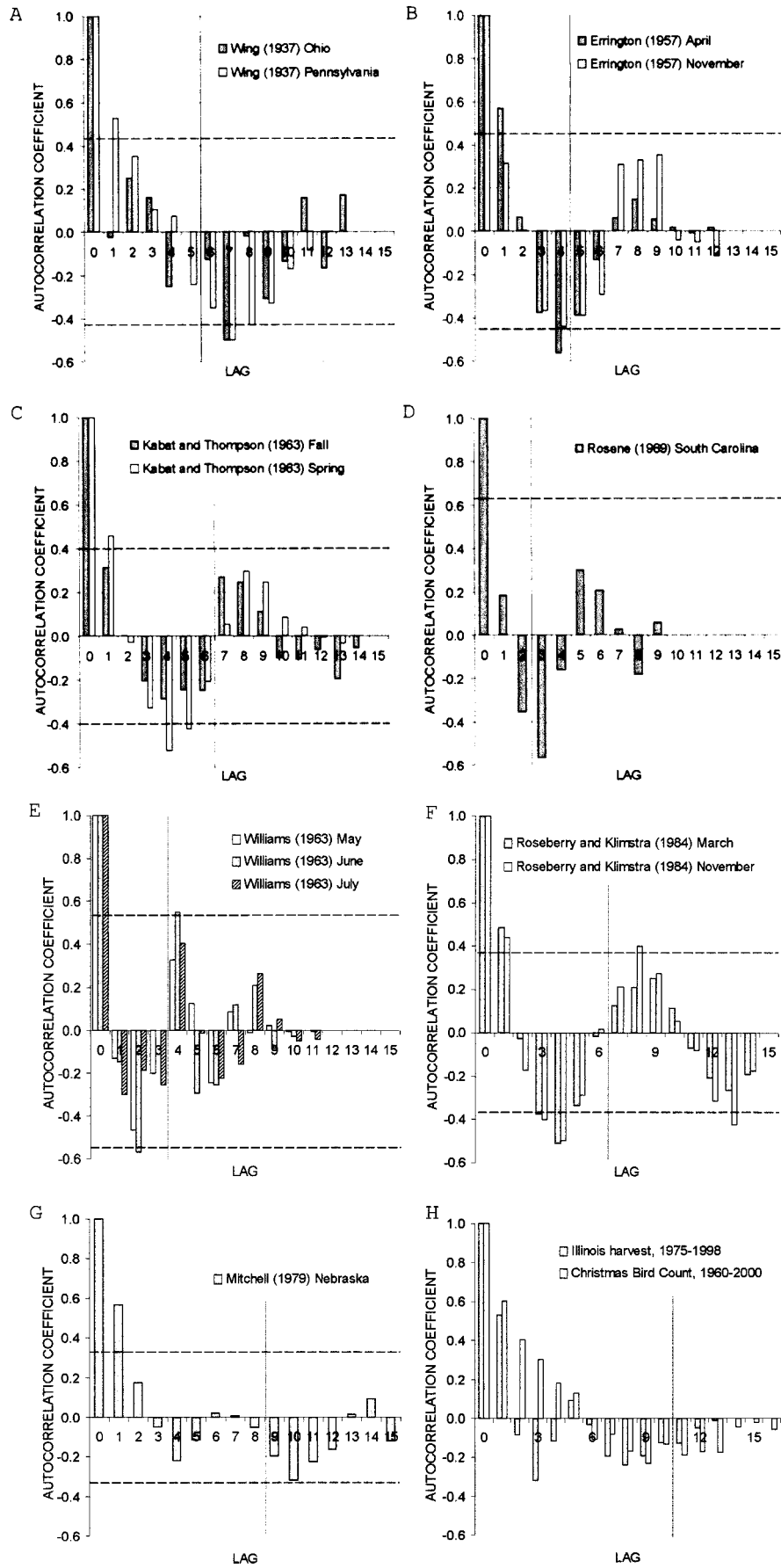
not significant. These non-significant recurring patterns are described as quasi-cycles; when the periodic pattern recurs with regularity and similar (though non-significant) intensity at each peak and valley, this quasi-cycle is labeled phase-remembering. When the intensity declines with lag distance, the quasi-cycle is phase-forgetting. Time series with non-significant lags or no obvious patterns in either the ACF or PACF plots were identified as random.

The theoretical ACF and PACF equals zero at all lags for an independently and identically distributed (i.e., random) sequence. But, when conducting hypothesis tests at $\alpha = 0.05$ across an independent set of such series, 5% of samples would be expected to reject the null when in fact the null is true (Type I error). To demonstrate the degree of difference between the 73 bobwhite time series we drew 73 random time series. We examined ACFs for cyclic patterning in the random time series and then compared the bobwhite time series with the random time series by a 2-sample test for equality of proportions. The proportions tested were the proportion of cyclic or quasi-cyclic series in each time series group. We applied Yates’ continuity correction to our test calculation.

To discern whether cyclicity was due to exogenous or endogenous factors we examined partial autocorrelation plots. Following Turchin (1990), we identified whether a population exhibited direct- or delayed-density dependence. Direct density dependence was iden-

Fig. 2. Autocorrelation functions for published time series of northern bobwhite abundance (A, Wing 1937; B, Errington 1957; C, Kabat and Thompson 1963; D, Rosene 1969; E, Williams 1963; F, Roseberry and Klimstra 1984; G, Mitchell 1979; H, annual Illinois harvest and Christmas Bird Counts; I, 3 data sets from Brennan et al. 2000). All plots represent northern bobwhite abundance except for Williams (1963), which are for California Quail. The horizontal dashed lines are Bartlett’s line of significance; correlations exceeding this line are significant. Tentative lags located to the right of the vertical line. Refer to Table 1 for details.

NORTHERN BOBWHITE CYCLICITY



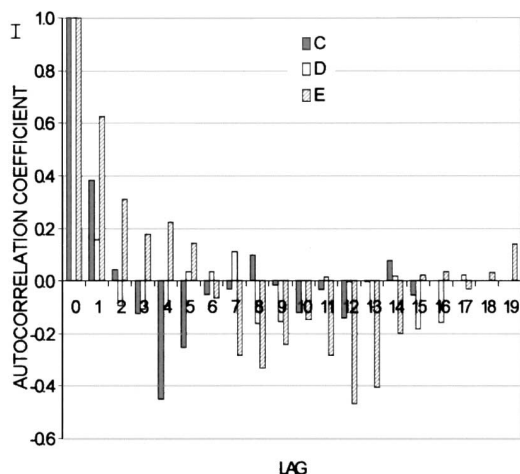


Fig. 2. Continued.

tified by a negative correlation between counts in year t and year $t-1$, whereas delayed density dependence was a negative correlation between year t and year $t-x$, where $x > 1$.

RESULTS

Illinois Data

At the time-scale we investigated ($n = 21-25$ yrs), examination of ACFs indicated periodicity in 18 of the 26 Illinois NABBS time series. None of the autocorrelations, however, exceeded Bartlett's band and, thus, no time series exhibited true cyclicity. Rather, the periodic patterns were quasi-cyclic.

The NABBS time series appeared to be grouped in 2 levels of quasi-periodicity (Fig. 1), 1 centered around a period of 7 years ($\bar{x}_T = 6.7 \pm 0.2$, $n = 6$), the other around a period of 17 years ($\bar{x}_T = 16.6 \pm 0.4$, $n = 10$). One other time series appeared to possess a period $T = 11$, whereas another time series was suggestive of periodicity $T > 20$.

Published Data Sets

Nine of 15 time series exhibited cyclical patterns (including data for the California quail), 8 of which were of the phase-forgetting quasi-cycle type (Fig. 2A-F). Periods varied considerably between 5 and 14 years (median = 8 yrs). The single instance of a definitively cycling time series ($T = 8$) was the autumn census for quail in southern Illinois (Fig. 2F; Roseberry and Klimstra 1984). Nebraska mail carrier observations, annual Illinois harvest, Christmas Bird Counts in Illinois, and coveys flushed/hour on 3 south Georgia plantations did not exhibit cyclicity (Fig. 2G-I).

Other North American Breeding Bird Survey Data Sets

Bobwhite populations as indexed by NABBS counts exhibited some form of cyclical patterning in a third of the states. Two states, Kansas and Kentucky,

possessed truly cyclic bobwhite populations (Fig. 3A). Kansas bobwhite cycled with a period of ~ 5.5 years, whereas bobwhite in Kentucky cycled on an 11-year period. Ten of the 27 remaining populations exhibited phase-forgetting quasi-cycles, similar to those of Ohio and Texas (Fig. 3B). As with the published data sets, periods varied considerably between 4 and 12 years (median = 6 yrs). Fifteen states, including Louisiana and Mississippi (Fig. 3C), exhibited little apparent periodicity.

There was a geographical gradient in cyclicity, as only northern and western populations exhibited regular variation in their abundance (Fig. 4). Based on state-level NABBS data, bobwhite in the southeastern United States demonstrated little propensity to cycle.

Comparison with Random Time Series

Fifteen of 73 time series possessed what we deemed quasi-cycles. The proportion of observed cycles ($P = 0.507$) versus expected cycles (as drawn from the random series, $P = 0.205$) was substantially greater ($\chi^2_1 = 50.6$, $P < 0.0001$). The random time series also differed from the bobwhite series in that none of the random time series exhibited true cyclicity and only 2 of the 15 random quasi-cycles were phase-forgetting, unlike the bobwhite quasi-cycles in which all were phase-forgetting.

Density Dependence

Partial autocorrelation function plots indicated delayed density dependence was not uncommon in bobwhite population dynamics though there were no instances of immediate density dependence. Seven of 18 (39%) published data sets ($\bar{x}_{lag} (\pm SE) = 4.7 \pm 1.0$), 10 of 25 (40%) Illinois NABBS routes ($\bar{x}_{lag} = 3.8 \pm 0.7$), and 9 of 30 (30%) state-level NABBS counts (including Illinois; $\bar{x}_{lag} = 4.0 \pm 1.1$) exhibited significant negative lags. Density dependence across all significant data sets was most common at lag 2 with a few significant lags as far out as 11 and 12 (grand $\bar{x}_{lag} = 4.1 \pm 0.5$). After accounting for deterministic trends in abundance, a significant lag at lag 2 indicated a steady-state population governed by density dependence increased or decreased for ≤ 2 successive years.

DISCUSSION

Approximately one-half of the time series we examined indicated cyclical behavior in bobwhite abundance, the predominant form of which was the phase-forgetting quasi-cycle. Only 3 of 73 (4%) time series exhibited truly significant periodicity. True cyclicity is a common phenomenon in boreal species such as various grouse (Keith 1963, Watson and Moss 1979, Williams 1985, Lindén 1988), hares (*Lepus* spp.; Sinclair et al. 1993), lynx (*Lynx lynx*; Keith 1963), and small mammals (Finerty 1980, Lindén 1988, Steen et al. 1990).

In quail, the evidence for cyclicity has been contradictory, both in the published literature and in the

NORTHERN BOBWHITE CYCLICITY

197

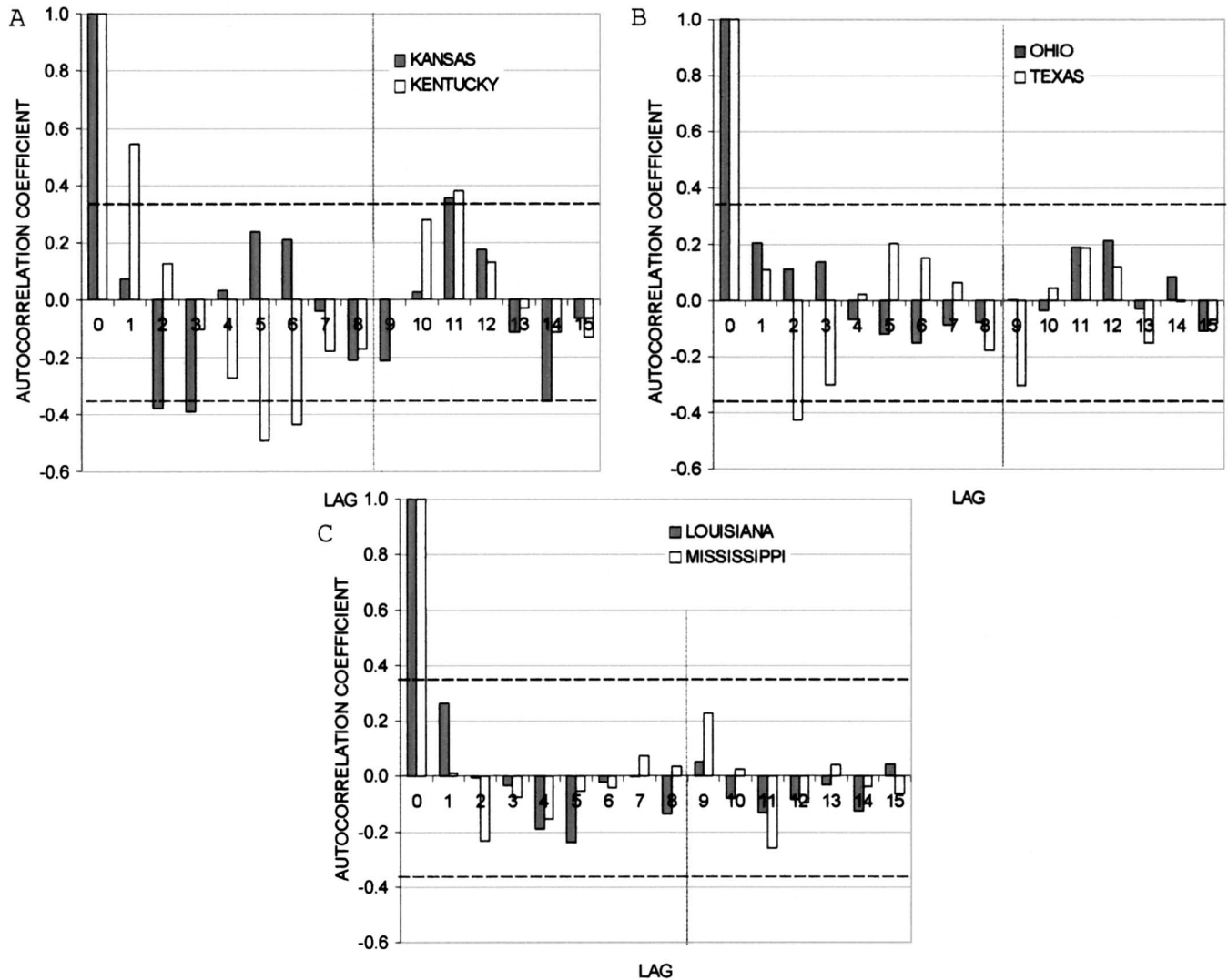


Fig. 3. Autocorrelation functions for cycling (Kans. and Ky.), quasi-cycling (Oh. and Tex.), and non-cycling (La. and Miss.) northern bobwhite populations, as determined from state-level counts of the North American Breeding Bird Survey. Autocorrelation function significant at $r = 0.336$; correlations at lags >8 are tentative due to decreased sample size.

data we analyzed. A solution for this seemingly contradictory behavior may lay in the geographical location and context of the population (Moss and Watson: In Press). Within similar latitudes, tetraonid species, for instance, exhibit both cyclic and non-cyclic dynamics (Moss and Watson: In Press). In small mammals and other taxa a biogeographical gradient occurs from north to south in amplitude and degree of cyclicality in population fluctuations (Dymond 1947, Lindén 1988, Bjørnstad et al. 1995, Turchin and Hanski 1997, Lambin et al. 2000). Because of this latitudinal gradient, true cyclicality is less common in non-boreal species.

Our analyses suggested most, but not all, of the northern and midwestern bobwhite populations exhibited periodicity in abundance. In contrast, populations in the southeastern United States exhibited no evidence for cyclicality.

In addition to latitudinal gradient, scale of analysis may be important in whether cycles are found when they exist (Moss and Watson: In Press). Watson et al.

(1998) found adjacent populations of rock ptarmigan (*Lagopus mutus*) in Scotland exhibited 6- and 10-year cycles. In bobwhite, route-level spring call counts and Roseberry and Klimstra's (1984) survey results indicated cyclicality in local population dynamics whereas regional-scale fall harvest and winter counts in Illinois did not. We believe neither fall harvest nor winter count data demonstrated cyclicality because the underlying cyclic patterns were obscured by averaging dynamics across different populations. When we examined time series of individual routes in Illinois rather than the mean state-wide NABBS, we discovered bobwhite commonly cycled at varying intervals, 17 years in central Illinois and 7 years in southern Illinois; the mean condition across routes obscured this pattern.

Similar north-to-south declines in period length were documented for voles and grouse (Moss and Watson: In Press). Angelstam et al. (1985) found voles cycled with a period of 5 years in northern Scandinavia, 3–4 years in central Scandinavia, and not at all in

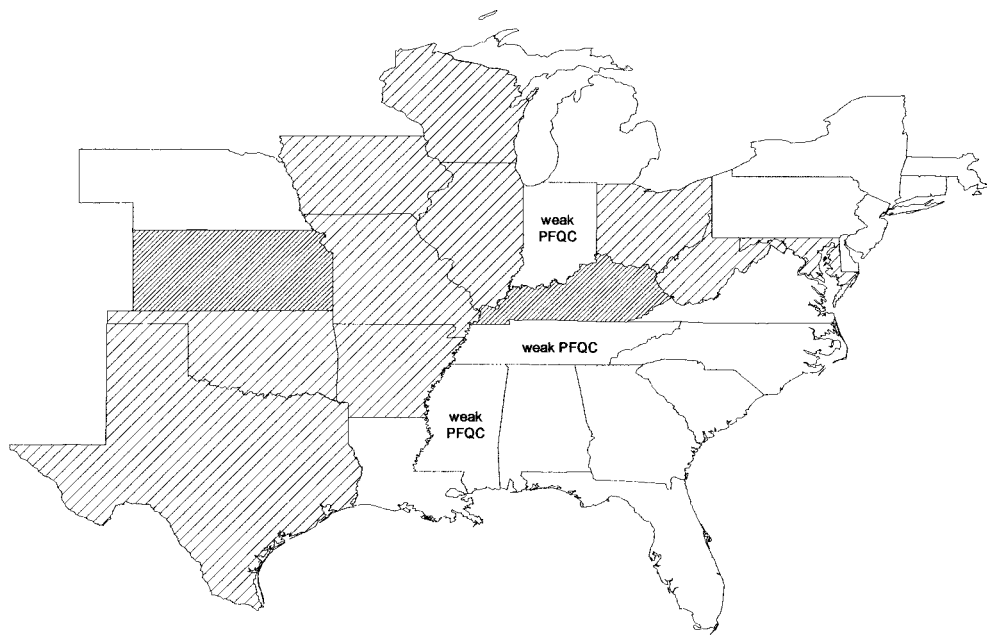


Fig. 4. Geographical gradient in the occurrence of cyclicity of northern Bobwhite as determined by North American Breeding Bird Survey data from 1967–2000 for states shown. Dark hatching indicates states where true cyclicity occurred in bobwhite abundance and light hatching indicates where bobwhite populations exhibited quasi-cyclicity. Bobwhite populations in states without hatching did not exhibit periodicity in abundance.

southern Scandinavia, whereas red grouse (*Lagopus lagopus*) cycled with periods of 7–8 years in Scotland and 4–5 years in England (Moss and Watson:In Press). Moss and Watson (In Press) suggested “regularities in weather patterns, possibly acting via plant growth, [may] entrain unstable populations to their periods.”

When cyclicity was evident in bobwhite it was generally of the phase-forgetting quasi-cycle type (PFQC; Nisbet and Gurney 1982, Turchin and Taylor 1992). Turchin and Taylor (1992) indicated deterministic population dynamics exhibiting either dampened oscillations around a stable point equilibrium, limit cycles, or “weak” chaos were sufficient to cause phase-forgetting quasi-cycles. We found that while some Illinois populations did exhibit the necessary chaotic dynamics to create phase-forgetting quasi-cycles, the number of populations that did so was small (~1%) and temporally inconsistent, and therefore an unlikely cause of cyclicity (Thogmartin 2001). So, how else may such complex patterns develop?

In a review of the causes of cyclicity, Kendall et al. (1999) indicated cycles may be caused by 1) direct and delayed-density dependence, 2) consumer-resource interactions such as predator-prey and host-pathogen, and 3) periodic environmental variation. Roseberry and Klimstra (1984) believed the cyclicity they observed was due to environmental forcings coupled with density dependence. Roseberry and Klimstra (1984) did not observe phase-forgetting, and thus their explanation was in line with Nisbet and Gurney’s (1982) periodically driven quasi-cycle. This phase-remembering pattern occurs in a deterministically stable system driven by periodic external fluctuations. They believed the periodic behavior of lunar illumination

and relatively evenly-spaced severe winter weather contributed to create cyclicity in their population.

Our analyses indicated, however, that the predominant cyclic pattern across the range of the species is phase-forgetting rather than phase-remembering. There are 3 recognized causes of phase-forgetting (Nisbet and Gurney 1982). Phase-forgetting quasi-cycles may be produced in a stable, underdamped system perturbed by either 1) demographic stochasticity (endogenous resonant quasi-cycle) or 2) aperiodic external fluctuations (exogenous resonant quasi-cycles). When the system is not stable, 3) environmental stochasticity may also promulgate PFQCs (perturbed limit cycles).

The question then is, which of the 3 causes of phase-forgetting likely explains bobwhite population dynamics? Inferring which of these processes may explain the observed PFQCs is difficult, as any or all of them may. If we can identify the bobwhite populations that we analyzed as stable or unstable, the problem becomes simpler. Stability, as Nisbet and Gurney (1982:11) defined it, is the long-term persistence of a population. By that definition, the various populations we examined were stable, if not stationary, narrowing our focus to endogenous and exogenous sources for cyclicity. Given that demographic stochasticity is most important only at small population sizes, our most parsimonious choice then becomes cyclicity due to external fluctuations. Kaitala et al. (1996) indicated occasional random perturbations reducing reproductive success may cause cyclicity in a population under delayed density-dependence. Delayed-density dependence was a common, though not universal phenomenon, in the northern and western states where cyclicity was evident. The random perturbations in these

states were likely stochastic climate extremes such as prolonged drought or extensive snowfall (Bridges et al. 2001, Thogmartin 2001). Therefore, we propose that cycles in bobwhite are likely due to the interaction of delayed density dependence and environmental perturbations. Given this proposed linkage between environmental perturbation and cyclicity in bobwhite dynamics, we might expect similar dynamics in western quail species (*Callipepla*) experiencing extremes in precipitation or temperature beyond the mean condition.

SUMMARY AND IMPLICATIONS

We established the frequency of occurrence, the geographical location, and potential mechanisms responsible for cyclicity in bobwhite. Two questions derive from these results. First, why did some northern and western populations cycle when others did not, and second, why do the periods differ between locations for those populations that do cycle?

Sixteen of the Illinois NABBS time series we examined were non-cyclic. If it is true that bobwhite populations generally unperturbed by climatic extremes, as in the southeastern United States, do not possess the necessary impetus for cyclic dynamics, then these 16 routes in Illinois may index populations buffered from climatic excess. Lack of cyclicity may also be due to a remaining degree of non-stationarity not removed by the detrending technique that we implemented.

Turchin and Taylor (1992) indicated non-stationarity may occur when there exists a lack of density dependence, externally driven periodic changes occur in the long-term mean abundance, or, if environmental change occurs on a time scale comparable to the length of the time series (≥ 25 yrs, in this case). Populations in the southeastern states, where bobwhite are experiencing their greatest decline, generally did not exhibit density dependence. When dynamics of bobwhite populations are not density dependent, populations may “randomly walk” away from the initial density, and thus do not possess a mean abundance around which to fluctuate (Turchin and Taylor 1992). This random walk is possible for bobwhite if abundance is constrained by factors other than conspecifics. Moss et al. (1996), for instance, were able to experimentally prevent population cycling in red grouse by increasing harvest when the population was on the upswing. By this rationale, bobwhite populations failing to exhibit cyclic patterns may be over-hunted during periods when the populations should be increasing.

Alternatively, non-stationarity in abundance may be due to fragmentation of habitat. Absence of cyclicity in snowshoe hares, tetraonids, and small rodents has been associated with fragmented habitat (Moss and Watson:In Press). This absence was attributed to increased mortality by generalist predators in these altered habitats and to increased dispersal into habitat where mortality exceeds reproduction (i.e., sinks). Fragmentation and loss of habitat is the primary cause associated with the decline of bobwhite indicating this

may be a more plausible hypothesis for lack of cyclic activity (Brennan 1991).

A multiplicity of processes integrating across temporal and spatial scales likely contributes to geographic differences in period length. One such source of variation is global climate patterns. For instance, El Niño Southern Oscillation events occur irregularly at intervals of 2–7 years, with the average about once every 3–4 years, whereas North Atlantic Oscillation events fluctuate on interannual and interdecadal time scales (Hurrell et al. 2001). In the midwestern United States, these global climate processes influence, for instance, seasonal temperature and precipitation, as well as corn production (Mauget and Upchurch 1999, Hurrell et al. 2001); Thogmartin (2001) showed with multivariate autoregressions that long-term bobwhite abundance in Illinois was associated with these climate processes. Both of these climatological phenomena, as well as other environmental processes, may interact to varying degrees across the bobwhite range to yield location-specific perturbations to demographic processes, causing cyclicity of varying period and strength.

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