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Analysing noisy time-series: describing regional variation in the cyclic dynamics of red grouse

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We develop a method for describing the periodicity of noisy ‘quasi-cyclic’ time-series based on integrals of their power spectra corresponding to different frequency intervals that we use to classify time-series as ‘strongly cyclic’, ‘weakly cyclic’ or ‘non-cyclic’. We apply this analysis to over 300 time-series of shooting records of red grouse from 289 moors located in 20 regions of the UK. Time-series from 63 of these populations were not distinguishable from white noise, but significant evidence of cyclic behaviour in the 2–15 year range was detected in time-series from 183 other populations. Time-series from the remaining 43 populations, though distinguishable from white noise, did not exhibit consistently recognizable cyclic behaviour in the same period range. Cyclic populations exhibit an average periodicity of 8.3 years, but only 20% of these populations cycle with a period of four to six years. Geographically, grouse populations are remarkable more for their dynamic heterogeneity than for any observable regularity. The relationship between the location of populations and their dynamical behaviour is weak. The prevalence of cyclic time-series within a region did not significantly differ from the overall average value. Moor region explained 22% of the variation in periodicity, differing from the overall mean in three regions. Average periodicity increases significantly from 6.8 to 8.9 years from the most southerly to most northerly populations. However, latitude explains only 5.3% of the variation in periodicity of the cycles.

Keywords: red grouse; quasi-cycles; regional dynamics; spectral analysis; time-series

1. INTRODUCTION

Ecologists have long been interested in the cyclic dynamics of vertebrate populations (Elton 1924; Kendall *et al.* 1999; Lindström *et al.* 2001). Probably the best known of these cyclic species are the snowshoe hare and lynx in Canada, the microtine rodents in Fennoscandia and Japan and the red grouse in the UK. Snowshoe hares, lynx and, to a lesser extent, microtines are examples of populations that fluctuate with a remarkably constant period (Elton & Nicholson 1942; Krebs & Myers 1974; Smith 1983; Stenseth & Ims 1993). Red grouse, however, appear to fluctuate variably, with peaks in abundance occurring somewhat irregularly both within and between populations (Potts *et al.* 1984; Williams 1985; Hudson 1992). Cycles with this pattern of uneven periodicity have been termed ‘phase-forgetting’ or ‘quasi-cyclic’ in contrast to precisely periodic cycles in which phase is perfectly remembered (Nisbet & Gurney 1982). However, an empirically operational framework with which to quantify and distinguish between quasi-cyclic and merely fluctuating dynamics is currently lacking.

Shooting records from a large number of grouse populations across the UK constitute time-series dating back from the present day for up to 160 years, but, to our knowledge, remain incompletely described, to date. The variation in dynamics contained within these data presents

both novel analytic challenges and a fascinating source of variance that requires explanation. The objectives of this paper are twofold: first, to develop methods that can rigorously quantify and categorize the oscillatory nature of time-series from each moor; and second, to use these methods systematically and consistently to describe regional variation in grouse population dynamics observed across populations.

The earliest assessments of red grouse shooting records were descriptive (Middleton 1934; Mackenzie 1952; but see Moran 1952). Fourteen time-series reported in these studies were subsequently subjected to individual autocorrelation analysis by Williams (1985), who showed that five exhibited statistically significant positive autocorrelation at lags of five and six years. Potts *et al.* (1984) examined 68 (unlogged) time-series from red grouse populations in the north of England and found only seven to exhibit significant positive autocorrelations at lags of greater than three years. The average periodicity of autoregressive models fitted to these cyclic time-series was 4.8 years (Potts *et al.* 1984). Hudson (1992) analysed 173 red grouse time-series from England and Scotland but found only a total of 27 autocorrelation coefficients for lags in the range 4–15 years to be significantly positive. This analysis was used to suggest that cycle period increases with latitude (Hudson 1992, fig. 24.4). All of these studies demonstrated a far higher frequency of significantly negative autocorrelation coefficients at shorter lags (half periods), which has been interpreted as evidence of quasi-cyclic ‘phase-forgetting’ dynamics.

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Table 1. Breakdown of the number of moors and time-series available from each of the 20 UK regions used in the analysis.

	region	number of time-series	number of moors	range in record length
1	Caithness, Sutherland	22	20	34–117
2	East Ross, West Highlands, West Ross	10	10	33–115
3	Argyll, Cunninghame, Islay	17	17	35–96
4	Monadhliath	13	13	33–111
5	Moray	14	14	36–122
6	Buchan, Donside	12	11	36–113
7	Breadalbane, Rannoch, Tummel	11	11	33–117
8	Cairngorm	8	8	32–109
9	Atholl	13	12	35–79
10	Angus, South Deeside	21	18	38–120
11	South Tayside	16	16	32–103
12	Trossachs	6	6	34–85
13	Lammermuir, Peebles, Pentlands and Moorfoots	12	11	32–83
14	Borders, Dumfries and Galloway, Lowther, Northumberland	39	33	33–126
15	North Dales	24	24	33–168
16	North York Moors	10	10	34–129
17	South Dales	25	23	33–155
18	Bowland	11	9	33–94
19	Peaks	21	17	32–115
20	Wales	7	6	32–110
	total	312	289	32–168

Two main hypotheses to explain these cycles have gained measures of theoretical and empirical support. The parasite hypothesis proposes that cycles are generated by parasite-induced reductions in host fecundity in conjunction with parasite-induced host mortality, the degree of parasite aggregation and stochastic effects (Dobson & Hudson 1992; Hudson 1992; Hudson *et al.* 1992, 1998, 2002). The kin selection hypothesis proposes that cycles are generated by delayed density-dependent changes in aggressiveness that influence territorial behaviour and the rate at which young males are recruited into the breeding population (Watson & Moss 1979; Watson *et al.* 1994; Moss *et al.* 1996; Moss & Watson 2001). These two hypotheses could potentially account for the differences in grouse population dynamics observed in different parts of the country. Hudson *et al.* (1992) have suggested that trends in the periodicity of grouse populations are consistent with plausible ranges of parameters implicit to the parasite hypothesis.

Despite widespread interest in these two hypotheses, the pattern of cyclic dynamics in red grouse populations in the UK remains to be fully described on the basis of all available data. The variable periodicity and amplitude exhibited by grouse populations through time complicates the characterization of their dynamics and precisely when a fluctuating population may be usefully termed cyclic is unclear (Nisbet & Gurney 1982). We develop a robust method to analyse power spectra to account for the noisy periodicity in the shooting-record data. The area under the spectrum of a time-series is directly proportional to the total variance in the time-series and spectral analysis allows examination of how this variance is accounted for by cycles of different periods (or frequencies). Noisy time-series might be said to cycle with several different periods simultaneously, so a method is required to determine when the observed variation in the time-series

accounted for by cycles of particular period is sufficient to characterize the time-series as cyclic with this period. We propose a method that objectively describes variability in periodicity and apply it to red grouse time-series in the UK. We focus this analysis on the higher-frequency oscillations present in the data for two reasons: first, because it is the low period cycles that have principally interested ecologists and for which mechanistic hypotheses have been proposed, and second, because longer-term trends are likely to have many possible explanations relating to management and land-use changes and their analysis will be deeply confounded with the detrending of data necessary for spectral analysis.

This paper uses red grouse shooting records from 289 populations located in 20 different regions across the entire range of red grouse in the UK to address the following three questions.

- (i) Are grouse time-series distinguishable from a simple white noise process?
- (ii) Do grouse time-series cycle according to the spectral criteria that we develop?
- (iii) What are the periodicities in any cycles and how do they vary geographically?

2. METHODS

(a) *Shooting records*

We analysed annual shooting records from 20 regions across England, Wales and Scotland. Time-series less than 32 years long were excluded, whereas time-series with contiguous gaps of four or more years were either split into series of at least 32 years in length (if possible) or excluded from further analysis (if not), resulting in a set of 312 time-series from 289 populations (thus 21 populations had more than one time-series)—see table 1.

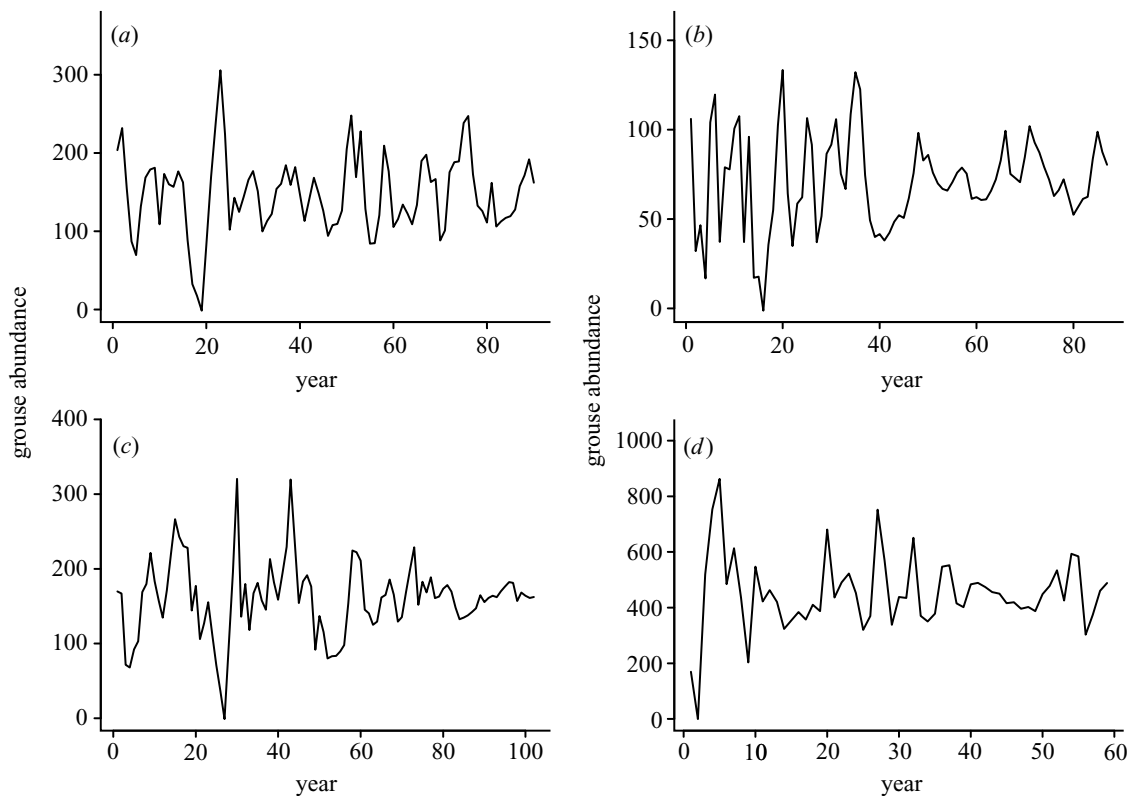


Figure 1. Examples of four detrended Box–Cox transformed time-series: (a) strongly cyclic with a period of eight years (moor 175); (b) non-cyclic (moor 227); (c) weakly cyclic with a period of seven years (moor 411; see § 2); and (d) indistinguishable from white noise (moor 2).

Time-series with gaps of three years or less were patched with log-linearly interpolated values. Prior to any analysis, long-term trends were removed from the time-series by subtracting a heavily smoothed copy of the same time-series. Smoothing was performed using the ‘supsmu’ smoothing function (Friedman 1984) as implemented in S-plus, including 25% of the observations in the smoothing window.

(b) Spectral analysis

Detrended time-series were normalized using the Box–Cox transformation (e.g. figure 1*a–d*) and then subjected to a Ljung–Box test on the first 15 autocorrelation coefficients to establish whether they were distinguishable from the null hypothesis of white noise (Ljung & Box 1978). We conducted spectral analysis on each time-series as described by Press *et al.* (1989) using the data-overlapping method to minimize the estimation variance for each spectral point (32 spectral estimates were obtained from each time-series, regardless of its length) and smoothed with a Parzen window. The analysis was confined to a limited range of the full spectrum corresponding to cycles of between 2 and 15 years’ length.

Having estimated the spectral density as a function of cycle frequency, $f(\omega)$ (figure 2*a*), we rescaled the spectral density as a function of period, $f(p=1/\omega)$ (figure 2*b*) and the quotient $f_{x-y} = \int_x^y f(p) dp / \int_2^{15} f(p) dp$ was estimated (figure 2*c*). This quotient was interpreted as the variation in the time-series that was accounted for by cycles of a period ranging from x to y years, expressed as a fraction of that accounted for by cycles of 2–15 years in duration. A cycle bandwidth k was defined to be equal to $y-x$. We calculated f_{x-y} for all bandwidths between one and three years inclusive for $x=1 \dots 15-k$. Let $E[f_{x-y}]$ be the expected value of f_{x-y} if the time-series is pure white noise (i.e. all period-

icities in the range 2–15 years present at equal amplitude). Define $\Phi(x)_k = f_{x-y} - E[f_{x-y}]$. Let $\Phi(\hat{x})_k = \max(\Phi(x)_k)$ (where the maximum is taken over all values of x and k). If $\hat{x} \geq 2$ or $\hat{x} + k < 15$ and $\Phi(\hat{x}-1)_k < \Phi(\hat{x})_k > \Phi(\hat{x}+1)_k$ then $\Phi(\hat{x})_k$ is said to be an ‘interior principal peak’. If $\hat{x} + k = 15$ then $\Phi(\hat{x})_k$ is said to be a ‘boundary peak’. If $\Phi(\hat{x})_k$ is an interior principal peak we define the time-series as ‘strongly cyclic’ with period $\hat{x} + k/2$ (figure 2*d*). If there are no interior peaks then the series is termed ‘non-cyclic’ within the 2–15-year window examined (figure 2*e*). If $\Phi(\hat{x})_k$ is a boundary peak but there is also a lower interior peak, $\Phi(x')_k$, corresponding to a shorter period than $\Phi(\hat{x})_k$, then the series is termed ‘weakly cyclic’ with period $x' + k'/2$ (figure 2*f*).

The significance of $\Phi(x)_k$ values was established as follows: given the statistical independence and the distribution of each estimate of the unsmoothed periodogram (which is χ^2 -distributed; see Diggle (1988)), we used Fisher’s combined probabilities method (Fisher 1954) to test the hypothesis that the set of periodogram estimates within the identified bandwidth ($x-y$) were significantly higher (at the 5% level) than the average value expected from white noise. We restrict reporting of results to the largest peaks judged significant using this methodology.

(c) Regional analysis

Each moor was assigned a Northing (y)- and Easting (x)-coordinate corresponding to a point within 1 km of the centre of the moor. The area of each moor was estimated by land-owners during two postal surveys undertaken in 1979 and 1985 (Hudson 1992). Logistic regression was used to analyse whether changes in the x - and/or y -coordinate affected the proportion of populations that were cyclic. Standard regression analyses were performed to examine the relationship between x - and y -coordinates

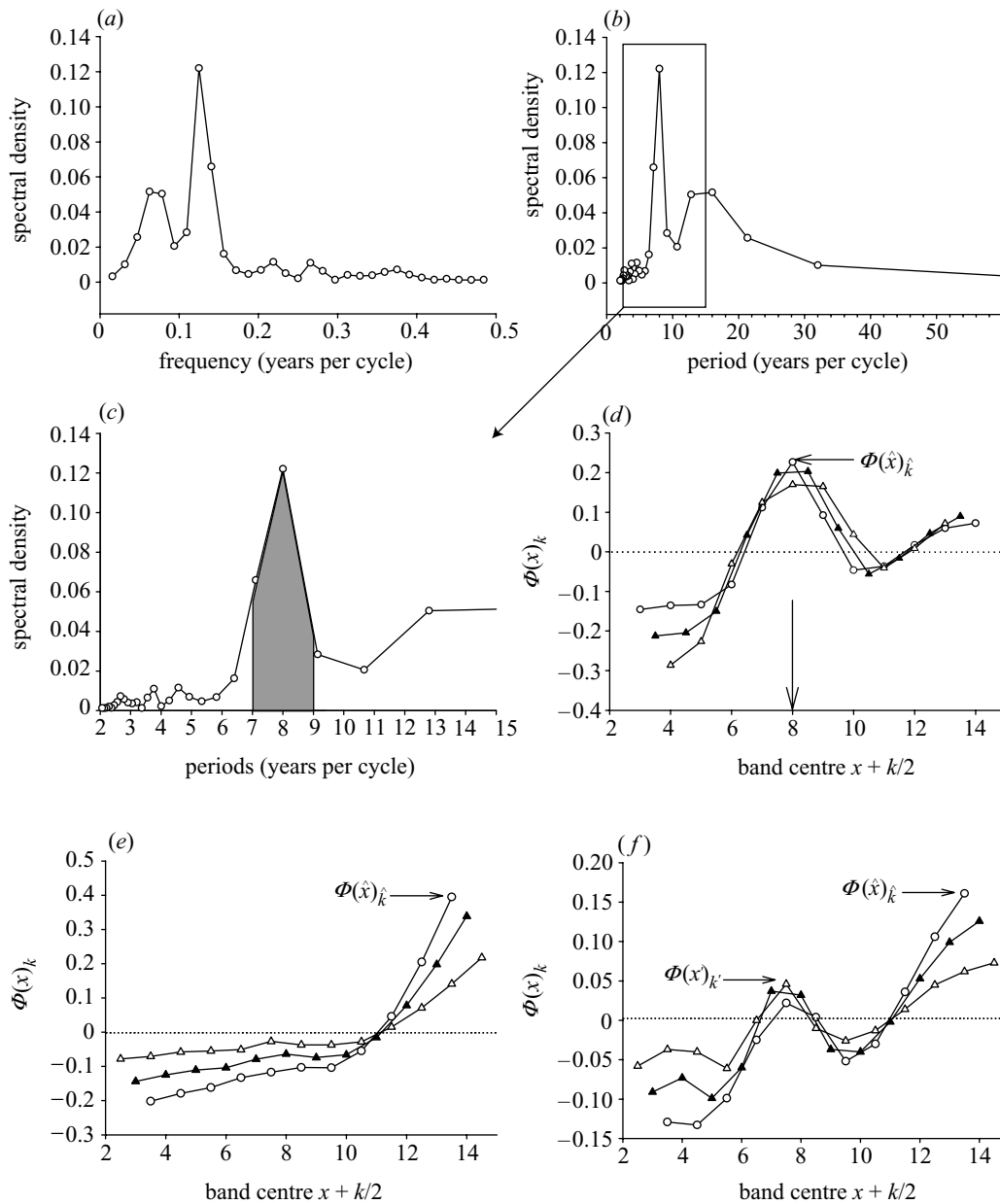


Figure 2. (a) An example of a spectrum plotted against frequency; (b) the same spectral estimates plotted with 1/frequency on the x -axis (note the bunching of points at low periods); (c) enlargement of the spectrum over the range corresponding to cyclic behaviour of periods of 2–15 years and the largest f_{x-y} value which in this case is $f_{7-9} = 0.391$. (d) Values of $\Phi(x)_k$, showing $\Phi(\hat{x})_k$ is an interior peak corresponding to an average 8-year cycle. (e) The $\Phi(x)_k$ profile of another spectrum where $\Phi(\hat{x})_k$ is a boundary peak, but no interior peak exists, therefore this population is non-cyclic in the 2–15-year range examined. (f) The $\Phi(x)_k$ profile of a final spectrum where $\Phi(\hat{x})_k$ is a boundary peak, but a clear interior peak exists, thus this population is classified as weakly cyclic with a period of 7.5 years.

and the period corresponding to the principal peak. In all cases, the potentially confounding relationship between moor area and moor coordinates was first taken into account.

3. RESULTS

(a) Dynamic behaviour

Only 54 time-series were characterized by at least one significant and positive autocorrelation coefficient corresponding to lags of between 4 and 15 years. Time-series from 63 of the 289 populations (21.8%) were statistically indistinguishable from white noise based on the Ljung–Box test (at the 5% level). Within the populations with

more than one time-series, 10 (of 21) had at least one of the time-series distinguishable from white noise and at least one not. The power of the Ljung–Box test increased with the length of the time-series (59 time-series shorter than the median length were indistinguishable from white noise, compared with only 19 of those greater than the median length).

While we focus here on the spectral properties relating to periodicities of between 2 and 15 years, it is noteworthy that, even after detrending the data, this portion of the spectrum only accounted for an average of 37% (range: 2–94%, figure 3a) of the total power of the time-series, and the largest spectral estimate corresponded to apparent

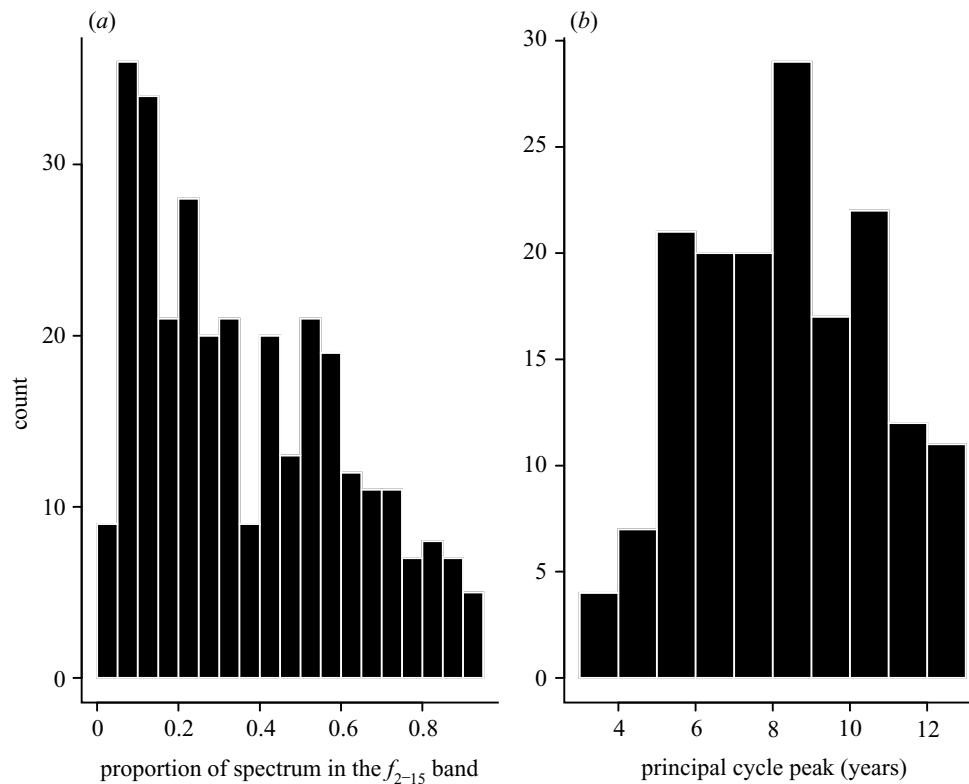


Figure 3. (a) The count distribution of the proportion of the total variance of the detrended time-series accounted for by cycles of periods of 2–15 years; (b) the count distribution of the periods of 146 populations judged to be strongly cyclic.

cyclic periods of more than 15 years for 79 of the 312 series.

We present the results derived from estimation of $\int_x^y f(p) dp$ in tables 2 and 3. Shooting records from 146 out of 289 (50.57%) populations were identified as strongly cyclic. The average principal peak period of these 146 populations was 8.3 years (minimum = 3.5 years, maximum = 13 years; figure 3b). Thirty-seven populations were identified as weakly cyclic (average = 7.1 years, minimum = 3.5, maximum = 10). Thus 183 (63.3%) populations can be said to be cyclic. Combining the white noise results and those populations with no identifiable peak gave 94 out of 289 (32.5%) populations classified as non-cyclic. The remaining 11 populations with multiple time-series exhibited one time-series that was strongly cyclic and the other non-cyclic.

The average bandwidth for cyclic populations was 2.54 years. Only 24 of the 183 cyclic populations were optimally described using a bandwidth of a single year, reflecting the noise surrounding the underlying periodicities in these data.

(b) Regional variation

The interpretation of this analysis is complicated by the significant positive relationship between the y -coordinate of a moor and the log of moor area ($t = 8.06$, $p < 0.001$), the significant negative relationship between the x -coordinate of a moor and log of moor area ($t = -5.32$, $p < 0.001$) (i.e. larger moors were found in the northwest part of the UK) and the significant relationship between the x - and y -coordinates of the moors ($t = -12.95$, $p < 0.001$): moors lie on a southeast–northwest axis. However, there were no significant relationships between the principal

peak period of cyclic populations and log of moor area ($t = -0.764$, $p = 0.446$, $r^2 = 0.003$); or between the proportion of populations that were cyclic (weakly plus strongly) and log of moor area ($\chi^2 = 3.67$, d.f. = 1, $p = 0.055$). In addition, there was no significant relationship between the length of time-series and moor locations ($t = 0.227$, $p < 0.821$ and $t = 1.684$, $p < 0.093$ for x - and y -coordinates, respectively).

There were no significant relationships between the proportion of populations that were cyclic (weakly plus strongly) and either their y -coordinate ($\chi^2 = 0.582$, d.f. = 1, $p = 0.446$) or x -coordinate ($\chi^2 = 2.220$, d.f. = 1, $p = 0.136$). In addition, there was no significant relationship between the proportion of populations that were cyclic and region ($\chi^2 = 21.861$, d.f. = 19, $p = 0.292$; see figure 4a). The proportion of cyclic populations in the Highlands (regions 1–12, 105/153 = 68.6%) did not differ from that in England (regions 15–19, 51/78 = 65.4%; $\chi^2 = 0.246$, d.f. = 1, $p = 0.617$).

There was a significant, albeit noisy positive relationship between how northerly a moor was and the principal peak period ($F_{1,181} = 10.19$, $p < 0.002$, $r^2 = 0.053$). There was no relationship between how far east a moor was and principal peak period ($F_{1,181} = 0.452$, $p = 0.463$) after the effect of latitude was accounted for. A better fit to principal peak period was obtained using moor region ($F_{19,163} = 2.406$, $p = 0.002$, $r^2 = 0.219$), with regions 17 (South Dales) and 18 (Bowland) individually exhibiting average principal peak periods significantly lower ($t > -2.99$, $p < 0.004$) and region 10 (Angus, South Deeside) significantly higher ($t = 1.99$, $p = 0.048$) than the overall mean peak value (figure 4b). Furthermore, Highland populations exhibited significantly longer cycles (mean = 8.53 years) compared

Table 2. Classification of populations and time-series as strongly, weakly and non-cyclic, together with associated periods computed using $\int_x^y f(p)dp$.

moor/time-series behaviour	time-series		moor ^a	
	count	details	count	details
white noise	78	—	63	—
strongly cyclic	163	mean peak = 8.41 (s.d. = 2.27)	146	8.33 (2.24)
weakly cyclic	38	7.13 (1.46)	37	7.11 (1.45)
cyclic	201	8.17 (2.20)	183	8.11 (2.16)
non-cyclic (and not white noise)	33	—	31	—
percentage of all moor cyclic	64.4	—	63.3	—
moors with strongly cyclic and non-cycling time-series	—	—	11	—

^a Populations with more than one time-series are only included if all time-series from the moor are classified the same way, i.e. if a moor has two time-series and one time-series is non-cycling (either from the Ljung–Box test, or because there was no distinct peak in the spectrum) and the other is strongly cycling then this moor is excluded from these numbers and is provided in table 3.

Table 3. Results where within-moor results differ.

moor	13	39	81	555	604	741	800	809	1035	1104	87 031
strongly cycling	1	1	1	1	1	1	1	1	1	1	1
non-cycling	1	1	1	1	1	3	1	1	1	1	1

with English populations (mean = 7.25 years, $F_{1,154} = 13.36$, $p < 0.001$, $r^2 = 0.080$). A summary of the identified dynamic behaviour associated with each moor is provided in figure 5.

4. DISCUSSION

The red grouse shooting records analysed here are among the most extensive ecological time-series in existence, encompassing nearly 300 locations with records of between 32 and 168 years' duration. Several workers have previously analysed these records but have tended to use either fairly restricted subsets of data or less powerful statistical analyses (Middleton 1934; Mackenzie 1952; Potts *et al.* 1984; Williams 1985; Hudson 1992).

The method adopted here for describing the cyclic status of red grouse populations identified a period interval from the spectrum that can capture the greatest variance relative to that expected from white noise. This procedure requires that the data be detectably periodic; in contrast to methods that, in the absence of significant positive autocorrelation, use significant negative autocorrelation at what are assumed to be half periods. In order to capture cyclic fluctuations with noisy periods, any form of sliding-window or sufficiently 'smoothed' analysis of the autocorrelogram, periodogram or spectrum should yield roughly equivalent results. Such methods have previously been applied to measles data (Bolker & Grenfell 1995). They are, in essence, an analysis of variance, the f_{x-y} bands reflecting the fraction of the total variance—represented by the area under the spectrum—accounted for by cycles of periods x to y years long. Our analysis identifies populations as cyclic with a specific period if less of their variation can be accounted for by periods slightly longer and shorter than this specified period. The absolute level of variance accounted for by any period is not taken directly

into account, as long as it is above the average level expected from a white noise process. Nisbet & Gurney (1982) have suggested that the coherence number, defined as the number of cycles over which the amplitude of the oscillations in the autocorrelation function decays by a predetermined factor, be used to characterize the 'amnesia' of phase-forgetting quasi-cycles. While conceptually attractive, precisely how to implement this idea for very noisy time-series characterized by autocorrelation functions lacking regular form is unclear.

The approach that we used to investigate the spectral pattern in red grouse shooting records identifies 63% of populations as cyclic while 22% were not distinguishable from white noise. The remaining 15% of populations either contributed multiple time-series that could not be consistently classified, or exhibited dynamics that could not be defined as cyclic by our analysis but were distinct from white noise. These populations were characterized by spectra that increased over the frequency range corresponding to fluctuations of periods of 2–15 years and therefore possessed only boundary peaks.

Cycling grouse populations are remarkable more for their dynamic heterogeneity than for any observable regularity. Strongly cyclic populations exhibit an average periodicity of 8.3 years and only 20% showed a period between four and six years. Our analysis focused on the spectral properties of time-series relating to cycle lengths of 2–15 years as it is these relatively high-frequency fluctuations that have historically been of most interest to ecologists (e.g. Hudson *et al.* 2002; Moss & Watson 2001). It is noteworthy, however, that this portion of the spectrum accounted for an average of only 37% of the power of the time-series and the largest spectral estimate corresponded to cycle periods of more than 15 years for 25% of available time-series. In other words, spectral analysis attributes a substantial fraction of the total vari-

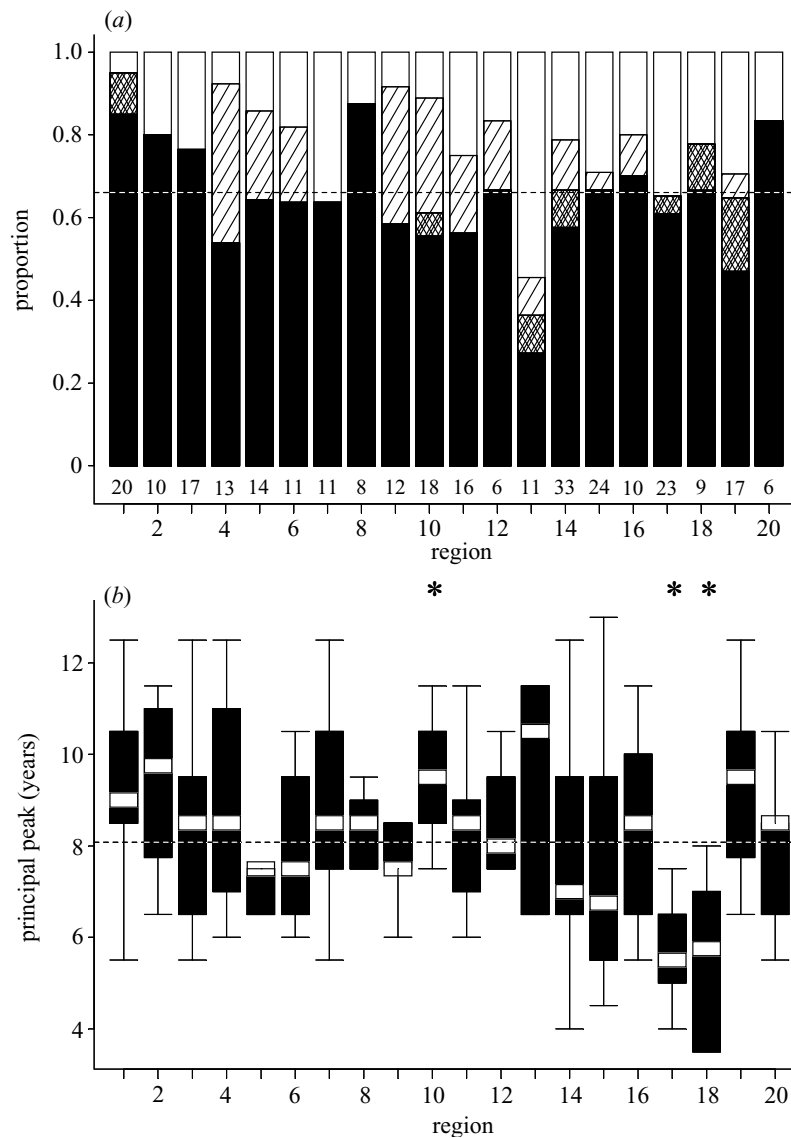


Figure 4. Regional variation in the dynamics of red grouse populations across the UK. (a) The proportion of populations from each region (see table 1) on which populations are judged to be cyclic (black), non-cyclic (hatched), indistinguishable from white noise (white) or from which multiple time-series are recovered that are classified in more than one category (cross-hatched). The number of populations in each region are indicated below each column. (b) The distribution of periodicities detected in time-series from different regions (white bars correspond to the median periodicity for each region, black bars the inter-quartile range and the lines the regional range of periodicity). Asterisks indicate deviation from the overall mean at the 5% level. Region numbers correspond to those reported in table 1.

ance in many of these time-series to low-frequency oscillations. It is possible that this reflects real long-term fluctuations in the data that detrending has failed to remove, but there are no obvious explanations for oscillations over these time-scales and they may not reflect phenomena of any intrinsic biological interest. For example, little is known about how irregularities in the data influence spectral estimation. In this respect, structural heterogeneities within the time-series were particularly apparent over the years of the First and Second World Wars. Moreover, heteroscedasticity or occasional extreme values may complicate the estimation of the spectrum. Similar low-frequency peaks have been observed in spectra from other noisy time-series (Bolker & Grenfell 1995) and may be a phenomenon widespread in ecological time-series (Halley 1996).

Spectral analysis requires that time-series be stationary and contain no long-term trends. Detrending removes variance from the time-series attributable to longer-term processes acting on the dynamics. However, an obvious difficulty arises when no *a priori* information exists as to which sources of variation should be removed and which left in. For example, linear long-term trends in the data can be easily removed by simple regression. Alternatively, the data could be much more closely detrended by removing a short-term moving average (differencing the data is equivalent to subtracting a second-order moving average). However, the more closely time-series are detrended the less low-frequency variance will remain and the greater proportion of the remaining variance will derive from higher-frequency sources. Data that have had all of the lower-frequency variance filtered out must, by definition,

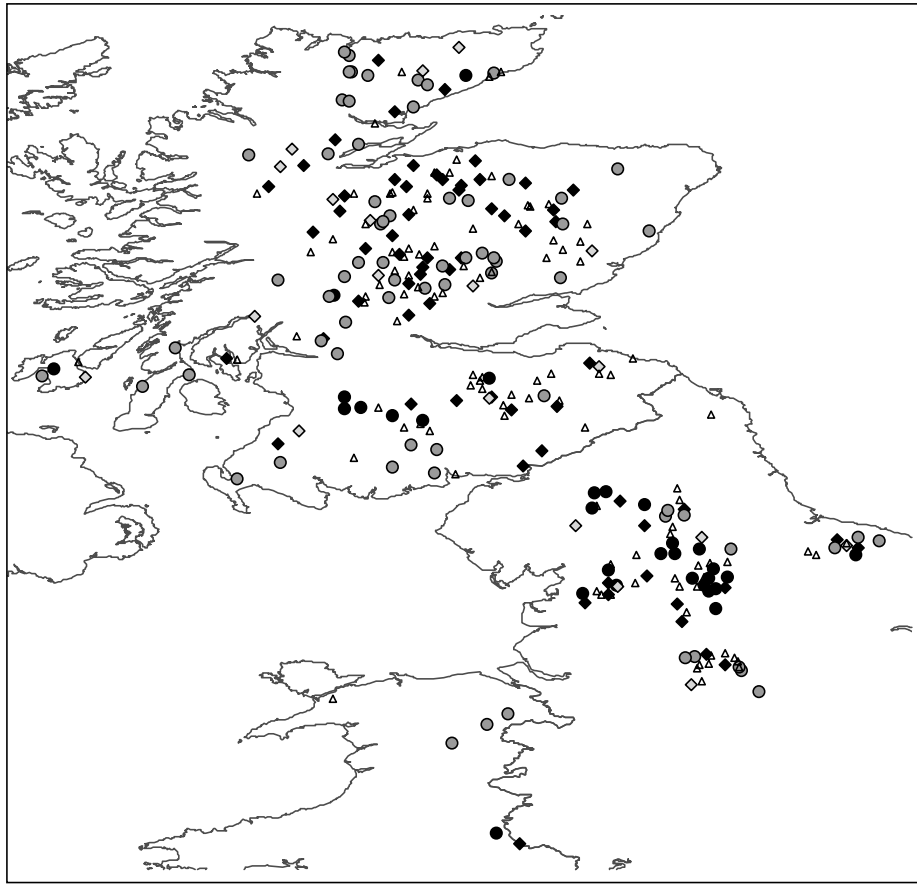


Figure 5. Map showing the location of moors and the dynamic behaviour of populations included in the analysis (black circles, period 3.5–5.5; black diamonds, period 6.0–8.0; grey circles, period 8.5–10.5; grey diamonds, period 11.0–13.0; triangles, non-cycling). Non-cyclic populations include those indistinguishable from white noise.

appear to oscillate at the frequency of the only variance remaining. Thus, it is important to avoid the creation of artificial peaks in the spectrum that could arise simply because all of the variance attributable to lower-frequency fluctuations has been removed by the detrending procedure. Our strategy has been to detrend the time-series to remove only the lowest-frequency noise and retain variance attributable to intermediate frequencies. We run the risk of failing to identify some populations in which cycling is obscured by lower-frequency noise, but we avoid creating cyclic populations simply as a consequence of creating peaks by filtering out low-frequency components of the spectrum.

The wide geographical area over which shooting records were available allowed us to investigate some of the regional patterns of red grouse cyclic dynamics across its distributional range. There were no consistent patterns in the proportion of cyclic populations within the 20 regions analysed. However, a significant relationship between moor location and periodicity was observed, in agreement with the conclusions of a previous study (Hudson 1992). The shortest period cycles were encountered in the Yorkshire Dales and Bowland (regions 17 and 18 with an average periodicity of 6.4 and 5.6 years, respectively) and the longest in Angus and South Deeside (region 10 with average periodicities of 9.2 years). Overall, region accounted for 22% of the variation in the observed period. However, average principal periodicity increased from only 6.8 to 8.9 years from the most southern to the most northern

regions—and this relationship was extremely noisy—with latitude explaining only 5.3% of the variation in periodicity. More complex multivariate analysis of the spatial variation observed in the spectra (as described by Bjornstad *et al.* (1996, 1998)) indicated no additional features of the spectra other than period that were more clearly related to the location of the populations.

We conclude that there is considerable variation in the period of red grouse cycles in the UK, and while only a small amount of this variation corresponds directly to latitude, a great deal more may be attributed to complex regional effects. It is simplistic to suggest either that there is a consistent geographical gradient of increasing periodicity in red grouse cycles with increasing latitude in the UK or that English grouse populations are characterized by four- to five-year cycles, whereas Scottish grouse populations vary from 6–10-year cycles.

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REFERENCES

- Bjornstad, O. N., Champely, S., Stenseth, N. C. & Saitoh, T. 1996 Cyclicity and stability of grey-sided voles, *Clethrionomys rufocanus*, of Hokkaido: spectral and principal components analyses. *Phil. Trans. R. Soc. Lond. B* **351**, 867–875.
- Bjornstad, O. N., Stenseth, N. C., Saitoh, T. & Lingjaerde, O. C. 1998 Mapping regional transitions in dynamics of *Clethrionomys rufocanus*: spectral densities and functional analysis. *Res. Pop. Ecol.* **40**, 77–84.
- Bolker, B. & Grenfell, B. T. 1995 Space, persistence and dynamics of measles epidemics. *Phil. Trans. R. Soc. Lond. B* **348**, 309–320.
- Diggle, P. J. 1988 *Time-series: a biostatistical introduction*. Oxford Science Publications.
- Dobson, A. P. & Hudson, P. J. 1992 Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. II. Population models. *J. Anim. Ecol.* **61**, 487–498.
- Elton, C. S. 1924 Periodic fluctuations in the numbers of animals: their causes and effects. *Br. J. Exp. Biol.* **2**, 119–163.
- Elton, C. S. & Nicholson, M. 1942 The ten-year cycle in numbers of the Lynx in Canada. *J. Anim. Ecol.* **11**, 215–244.
- Fisher, R. A. 1954 *Statistical methods for research workers*, 12th edn. Edinburgh: Oliver & Boyd.
- Friedman, J. H. 1984 A variable span smoother. Technical Report no. 5, Laboratory for Computational Statistics, Stanford University, CA.
- Halley, J. M. 1996 Ecology, evolution and 1/f-noise. *Trends Ecol. Evol.* **11**, 33–37.
- Hudson, P. J. 1992 *Grouse in space and time*. Fordingbridge, UK: Game Conservancy Trust.
- Hudson, P. J., Dobson, A. P. & Newborn, D. 1992 Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. I. Monitoring and parasite reductions experiments. *J. Anim. Ecol.* **61**, 477–486.
- Hudson, P. J., Dobson, A. P. & Newborn, D. 1998 Prevention of population cycles by parasite removal. *Science* **282**, 2256–2258.
- Hudson, P. J., Dobson, A. P. & Newborn, D. 2002 Population cycles in red grouse. In *Population cycles* (ed. A. Berryman), pp. 109–129. Oxford University Press.
- Kendall, B. E., Briggs, C. J., Murdoch, W. W., Turchin, P., Ellner, S. P., McCauley, E., Nisbet, R. M. & Wood, S. N. 1999 Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology* **80**, 1789–1805.
- Krebs, C. J. & Myers, J. H. 1974 Population cycles in small mammals. *Adv. Ecol. Res.* **8**, 267–299.
- Lindström, J., Ranta, E., Kokko, H., Lundberg, P. & Kaitala, V. 2001 From arctic lemmings to adaptive dynamics: Charles Elton's legacy in population ecology. *Biol. Rev.* **76**, 129–158.
- Ljung, G. M. & Box, G. E. P. 1978 On a measure of lack of fit in time-series models. *Biometrika* **65**, 297–303.
- Mackenzie, J. 1952 Fluctuations in the numbers of British Tetraonids. *J. Anim. Ecol.* **21**, 128–153.
- Middleton, A. D. 1934 Periodic fluctuations in British game populations. *J. Anim. Ecol.* **3**, 231–249.
- Moran, P. A. P. 1952 The statistical analysis of game bird records. *J. Anim. Ecol.* **21**, 154–158.
- Moss, R. & Watson, A. 2001 Population cycles in birds of the grouse family. *Adv. Ecol. Res.* **32**, 53–111.
- Moss, R., Watson, A. & Parr, R. 1996 Experimental prevention of a population cycle in red grouse. *Ecology* **77**, 1512–1530.
- Nisbet, R. M. & Gurney, W. S. C. 1982 *Modelling fluctuating populations*. Chichester: Wiley.
- Potts, G. R., Tapper, S. C. & Hudson, P. J. 1984 Population fluctuations in red grouse: analysis of bag records and a simulation model. *J. Anim. Ecol.* **53**, 21–36.
- Press, W. H., Flannery, B. P., Teukolsky, S. A. & Vetterling, W. T. 1989 *Numerical recipes: the art of scientific computing*. Cambridge University Press.
- Smith, C. H. 1983 Spatial trends in Canadian snowshoe hare, *Lepus americanus*, population cycles. *Can. Field Nat.* **97**, 151–160.
- Stenseth, N. C. & Ims, R. A. 1993 Population dynamics of lemmings: temporal and spatial variation: an introduction. In *The biology of the lemming* (ed. N. C. Stenseth & R. A. Ims), pp. 61–96. London: Academic.
- Watson, A. & Moss, R. 1979 Population cycles in the Tetraonidae. *Ornis Fennica* **56**, 87–109.
- Watson, A., Moss, R., Parr, R., Mountford, M. D. & Rothery, P. 1994 Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. *J. Anim. Ecol.* **63**, 39–50.
- Williams, J. 1985 Statistical analysis of fluctuations in red grouse bag data. *Oecologia* **65**, 269–272.

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