Spatial synchrony in red grouse population dynamics

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Introduction

Red grouse (*Lagopus lagopus scoticus*) are common in areas of heather moorland habitat in the British uplands where they have been actively managed for the purpose of sport shooting since the late 19th century. Many populations of red grouse exhibit unstable dynamics, often characterised by periodic fluctuations in population abundance. Red grouse population dynamics have been the subject of extensive study since the late 1950s. Time-series analysis of harvesting records from 289 red grouse populations suggested that red grouse fluctuate in 'phase forgetting quasi-cycles' with a variable period (Potts, Tapper & Hudson 1984).

There are currently two main hypotheses to explain these fluctuations. The parasite hypothesis (Hudson, Dobson & Newborn 1992, 1998), suggests that the parasitic trichostrongyle worm generates these cycles by reducing female fecundity and increasing mortality when grouse are present at high densities. The kin selection hypothesis (Moss & Watson 1985; Moss, Watson & Parr 1996) proposes that fluctuations are generated by delayed density-dependent changes in aggression and the rate at which young males are recruited into the population. Recent work suggests that an interaction between parasites and behaviour may be the main driver of unstable dynamics (Mougeot *et al.* 2005; Redpath *et al.* 2006).

We provide a description of patterns of synchrony in grouse population cycles across the UK. We ask the following questions:
1) Do red grouse populations fluctuate synchronously?
2) How does synchrony between pairs of populations change with the distance between them?
3) Can any potential processes driving synchrony in red grouse abundance be identified?
4) How is this synchrony maintained?

Patterns of synchrony

Harvesting records (number of grouse shot per year) from 304 UK moors, with series length per moor ranging from 32 to 168 years, were utilised to provide an indirect measure of grouse abundance. Cattadori *et al.* (2003) demonstrated that the relationship between log-harvest count and log-population density was linear with a slope close to unity, and therefore suggest this measure can be used as a suitable alternative to count data.

A matrix of cross-correlation coefficients was estimated, with each series compared to each other series. Bootstrap analysis of this matrix suggested weak but significant evidence of synchrony between grouse population cycles.

The matrix of cross-correlation coefficients was analysed with respect to a matrix of inter-moor Euclidean distance. Estimation of the spatial autocorrelation of grouse population dynamics across moors indicates high levels of synchrony between neighbouring moors, but that this declines sharply with increasing inter-moor distance. At distances of greater than 100 km, grouse series exhibit only very weakly positive cross-correlation coefficients.

For each series, we defined moor neighbourliness as a measure of the density of moors in the local area. For example, a moor in Wales is expected to have a low value for neighbourliness, given its isolated location and lack of other nearby moorland patches. Conversely, a moor in Perthshire in Scotland is expected to have a high value for neighbourliness, given the increased density of surrounding moors. A mean cross-correlation coefficient (termed local synchrony) was calculated for each series, weighted by the inter-moor distance, to represent the degree to which each moor is in synchrony with other nearby moors. There was a statistically significant relationship between local synchrony and neighbourliness ($p < 0.001$).

28 geographical, environmental and other candidate variables were examined to construct a general linear model to explain variation in local synchrony. Of these, five explained significant levels of variation in synchrony: grouse moor productivity (average size of shooting bag), distance from the Atlantic coast moving in a north-easterly direction, April and June temperatures, and increasing June rainfall (Table 1).

Table 1. Variables explaining patterns of local synchrony in cycles of grouse moor abundance (Type III SS).

Variable	Relationship to synchrony	Significance
Moor neighbourliness	Neighbourly moors show increased synchrony	<0.0001
Average grouse bag	Productive moors show increased synchrony	<0.0001
North-easterly position	Synchrony increases as moors are located further from the Atlantic Coast	<0.0001
Average April temperature	High April temp. increases synchrony	<0.0001
Average June temperature	High June temp. decreases synchrony	0.001
Average June rainfall	Increased June rainfall increases synchrony	<0.0001

Processes driving synchrony

Hugueny (2006) suggests that both dynamic coupling between populations and correlation noise (the Moran effect) can explain spatial synchrony in population dynamics. Synchrony can be maintained through coupling that is continuous and weak, or intermittent and strong.

An alternative way to look at time-series data is to categorise each year according to state – when the population is at a peak, a trough, increasing or decreasing (Haydon *et al.* 2003). The set of populations at any time point can be characterised by the frequency distribution of these different states, and changes to this frequency distribution through time can be used to test the hypothesis that the dynamics of each population occurs

independently. Thus we can identify years in which populations converge into synchronous states.

Using this technique, we are able to identify particular years (approximately 1 in 6) in which grouse populations appear to be in greater synchrony than expected. This result supports the hypothesis that intermittent, strong coupling is driving grouse population synchrony.

Further work will attempt to identify the mechanisms through which coupling between populations might drive patterns of grouse synchrony.

Acknowledgements

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