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Summary

1. We examined 223 time-series of red grouse (*Lagopus lagopus scoticus*) numbers
compiled from shooting bag-records from grouse moors located across England,
Scotland and Wales for evidence of non-time-reversibility, asymmetry in cycle shape
and non-linearity.

2. We found 44% of time-series to be non-time-reversible. Over 80% of time-series spent
more time increasing than decreasing (but only 32% did so significantly).

3. Non-linearity was detected in 44% of time-series examined, and these non-linear
time-series were 1·7 times more likely to be non-time-reversible compared to the linear
time-series.

4. The occurrence of non-linear and non-time-reversible series was not related to
location, number of days with rain, temperature, moor area or population growth rate.
The predominance of symmetrical peaks increased with easting but was not related to
number of days with rain, temperature, northing or moor area.

5. There were no significant relationships between time-reversibility or non-linearity
status and either tendency to cycle or cycle periodicity. However, populations that
cycled with longer periods exhibited slower rates of increase and more equal lengths of
time increasing and decreasing in numbers.

6. Our results provide little evidence that grouse cycles observed in different parts of the
species range in the United Kingdom arise from fundamentally different processes.

Key-words: asymmetry, cycle shape, *Lagopus lagopus scoticus*, red grouse, time reversib-
ility, time-series analysis.

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Introduction

Compelling explanations for the cyclic population
dynamics observed in many vertebrate species remain
scant. Evidence for various hypotheses has come from
large-scale field experiments (e.g. Krebs *et al*. 1995;
Mougeot *et al*. 2003), studies of environmental features
that correlate with cyclic dynamics (e.g. Sinclair &
Gosline 1997), studies of the periodicity or amplitude

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of cycles through time-series analysis (e.g. Royama 1992)
or similarity between data and behaviour of models
that postulate plausible mechanisms (e.g. Turchin *et al*.
2000). Both Ginzburg & Inchausti (1997) and Turchin
et al. (2000) have also suggested that the shapes of
cycles themselves may contain information relating
to the underlying causal mechanisms. Simple trophic
models suggest that cycles with sharp pointed peaks
may reflect 'bottom-up' resource limitation, whereas
cycles that approach their peaks asymptotically before
falling away more quickly are expected to arise from
'top-down' regulation by natural enemies.

A more general property relating to the shape of
population cycles is whether they are laterally asym-
metrical (i.e. temporally directional, or appear identical
regardless of whether time is run forwards or back-
wards). Stone, Landan & May (1995) have found some
ecological time-series to be non-time-reversible, per-
mitting differentiation between linear and non-linear

explanations of underlying mechanisms. A linear time-series [for example, one generated using a linear auto-regressive (AR) model with Gaussian innovations] is time-reversible (Weiss 1975). Non-time-reversible time-series can be generated only from non-linear dynamics and rejection of time-reversibility indicates inadequacy of Gaussian AR processes to represent them. The presence of non-linear dynamics suggests density-dependent population regulation. Persistent cyclic population dynamics can be achieved with non-linear dynamics without requiring delayed density dependence when the density-dependent relationship itself changes with population density as, for example, is the case in a threshold autoregressive (TAR) process. If population density depends on past densities in a linear fashion, then persistent cyclic population dynamics can be achieved only through delayed density dependence extending back at least 2 years (e.g. by an AR process of at least 2nd-order).

Time-series analysis has revealed that cyclic dynamics are a consistent feature in some populations of red grouse (*Lagopus lagopus scoticus*) inhabiting moorland in the United Kingdom (Middleton 1934; Mackenzie 1952; Moran 1952; Hudson, Dobson & Newborn 1985; Williams 1985; Hudson 1992; Haydon *et al*. 2002). The ecological mechanisms underlying these cycles remain controversial, with two non-exclusive hypotheses attracting a degree of theoretical and empirical support. The kin selection hypothesis proposes that cycles are generated by delayed density-dependent changes in aggression which influence spacing behaviour and the rate at which young males are recruited into the breeding population (Watson *et al*. 1994; Matthiopoulos, Moss & Lambin 1998; MacColl *et al*. 2000; Moss & Watson 2001). The parasite hypothesis proposes that cycles are generated by parasite-induced reductions in host fecundity caused by the caecal nematode *Trichostrongylus tenuis* in conjunction with a low degree of parasite aggregation (Hudson *et al*. 1985; Hudson 1986a, 1992; Dobson & Hudson 1992; Hudson *et al.* 1998).

Research underpinning these two hypotheses has, until recently, been conducted in two different parts of the range of red grouse in the United Kingdom. The kin selection hypothesis is based primarily on research on dry, freely draining grouse moors in NE Scotland (Moss & Watson 2001 and references therein). Here observed population cycles have been described as symmetrical, with approximately equal periods of time spent in increase and decrease phases (Moss *et al*. 1993), an observation consistent with predictions of models of the kin selection mechanism of cyclic dynamics (Mountford *et al*. 1989; Moss & Watson 1991). In contrast, the parasite hypothesis is derived largely from research on wet heaths in Northern England (Hudson *et al*. 2002 and references therein). Here populations appear more 'saw-toothed' and asymmetrical, with longer periods in the increase phase, and faster population crashes following peak densities (Hudson *et al*. 1998), an observation consistent with predictions of models of the parasite mechanism of cyclic dynamics (Dobson & Hudson 1992; Turchin 2003). Moss *et al*. (1993) have suggested that these different cycle shapes may arise because the two proposed mechanisms apply to separate regions of the grouse range within the United Kingdom – a possibility we will refer to as the dual explanation hypothesis. The objective of the present paper is to describe grouse cycle shapes across the species range in the United Kingdom, evaluating the evidence for the dual explanation hypothesis.

The dual explanation hypothesis could arise if infection rates vary spatially with climatic or other conditions such that dynamics of some grouse populations are dominated by parasites while others are dominated by spacing behaviour. Strong support for the dual explanation hypothesis would be found if the dynamics of grouse populations covaried with the occurrence of nematode infections. Unfortunately, parallel longitudinal studies on intensity of *T. tenuis* infections from a series of contrasting populations in the United Kingdom are incomplete. However, there is evidence that grouse on dry freely draining heather moorland areas in Northern England have lower infection rates with *T. tenuis* than grouse on wetter blanket bog areas and that these differences are caused by variation in climate (Hudson *et al*. 1985). Dampness is a requirement for transmission and blanket bog develops a cover of *Sphagnum* moss that provides suitable conditions for transmission (Hudson *et al*. 1985; Saunders, Tompkins & Hudson 1999). On the drier freely drained heather moorland areas, annual variation in transmission is correlated with rainfall. (Hudson *et al*. 1985; Moss *et al*. 1993). A good ecological measure of wetness and one that reflects conditions suitable for infection is number of days per year with ≥ 1 mm of rainfall, referred to henceforth as rain days, where > 160 rain days per annum provides a reasonable threshold for blanket bog to develop (Hudson 1986b, 1992).

Grouse moors across the United Kingdom are known to vary in their productivity and the density of grouse populations that they can sustain (Hudson *et al*. 2002). Because the type and intensity of density dependence may vary both with average moor population density and maximum growth rates of populations, we might expect non-linearity and asymmetry to be associated more easily with faster growing and higher density populations, potentially confounding any association between patterns of parasitism, non-linearity and asymmetry. We therefore examined occurrence of asymmetry and non-linearity as a function of grouse population productivity and density.

To date, red grouse shooting records have not been directly examined for dynamical 'signatures' that might lend support for hypotheses proposed to explain their cyclic dynamics. Annual shooting records exist for 289 red grouse populations across the entire species range in the United Kingdom and date back to 170 years from the present day (Hudson 1992). In this paper we use these shooting records to address the following questions:

• What proportion of grouse time-series are asymmetrical and/or non-linear?
• How does asymmetry manifest itself within the time-series?
• Is there geographical variation in patterns of asymmetry and non-linearity?
• Are variations in patterns of asymmetry and non-linearity related to variations in grouse population density, growth and decline rates or with anticipated patterns in intensity of parasitism as predicted by rainfall?

Methods

DATA

The time-series used came from moors located in all the major regions of grouse habitats in the United Kingdom where shooting has occurred for at least 32 years. Two hundred and eighty-nine grouse time-series were included, de-trended and patched or split, as described in Haydon *et al.* (2002). We excluded from subsequent analyses those time-series that were not distinguishable (at the 5% level) either from white noise using the Ljung–Box test, or from a zero-th order autoregressive process (AR-0, see below). For nine populations there were multiple time-series of which none were either white noise or AR-0, and in these cases the longest time-series was selected for analysis. For the purposes of model fitting and non-linear analysis, time-series were normalized using Box–Cox transformations by taking the value of the exponent that was the maximum likelihood for each time-series (see Results) as described by Sokal & Rohlf (1981) and then standardized to zero mean and unit variance.

CYCLE SHAPE

Time reversibility

We applied Rothman's (1992) TR test to time-series to determine time-reversibility, which examines the equality of the bi-covariances $\sum_{t=k+1}^{T} x_t^2 x_{t-k} = \sum_{t=k+1}^{T} x_t x_{t-k}^2$ for various values of lag, k (where x_t is the transformed time-series, and T is the length of the time-series). This test requires that the time-series be represented as an AR(p) process: $x_t = b_0 + \sum_{i=1}^{p} b_i x_{t-i} + \varepsilon_t$ where p is the order of the AR process (for this test p must be non-zero). Model selection was that which minimized the normalized Akaike's information criteria (NAIC) (Tong 1993) and model order was limited to a maximum of 3rd-order (however, 2nd- and 3rd-order AR processes are still capable of capturing a very wide range of periodicities).

Ratio of increasing : decreasing grouse numbers

As a more direct and intuitive test of asymmetry we examined the ratio of 'increase' years ($x_{t+1} > x_t$) to

'decrease' years ($x_{t+1} < x_t$) within each time-series (as suggested first by Ginzburg & Inchausti (1997), and henceforth referred to as the GI ratio), and determined if this ratio deviated from 1 (using a two-tailed test at the 5% level) by examining the distribution of this same ratio in 1000 time-series of corresponding length simulated using the best-fitting AR process, as identified using NAIC.

The shapes of peaks

Grouse time-series have non-trivial non-linear long-term trends contained within them, particularly after the Second World War (e.g. Fig. 1a–f). This precludes interpreting a simple skewness based analysis of the logged data with regard to cycle shape. Therefore, we used the raw data to examine the approach of time-series to peaks and the decline from peaks, where peaks were defined as values that were preceded by at least 2 years of consecutive increase and proceeded by 2 years of consecutive decline. In the approach to peaks, we looked at the ratio of growth rates between years $t-2$ to $t-1$, and $t-1$ to t, for time-series peaking in year t. If the peak is reached in an asymptotic-like 'convex' fashion then the growth rates will decrease as the peak is approached, and the approach to the peak will be convex-shaped (Fig. 2a,b). Alternatively, if growth rates increase toward the peak, the approach to peaks will be concave-shaped (Fig. 2c,d). A similar methodology was adopted for the decline from peaks, where we looked at the ratio of decline rates between years t to $t + 1$, and $t + 1$ to $t + 2$. Within each time-series we identified the frequency of each type of peak shape (symmetrical – either convex approach, convex decline or concave approach, concave decline; and asymmetrical – either convex approach, concave decline or concave approach, convex decline), and then pooled these frequencies across all time-series by region.

Propensity to cycle and cycle period

Haydon *et al.* (2002) examined these same time-series for evidence of cyclic behaviour based on spectral analysis and classified each time-series as cyclic with specified period or as non-cyclic. This classification was used in this analysis.

GROWTH RATES AND POPULATION DENSITY

Population growth and decline rates

Positive and negative growth (hereafter termed decline) rates were calculated from raw data for each time-series as N_t/N_{t-1} (where N_t is number of grouse shot in year t). If either numerator or denominator were zero (449/21 094 data points), rates were excluded. We were interested in examining 'maximal rates', therefore we excluded the most extreme growth and decline rates and selected the 75th percentiles. These 75th percentiles
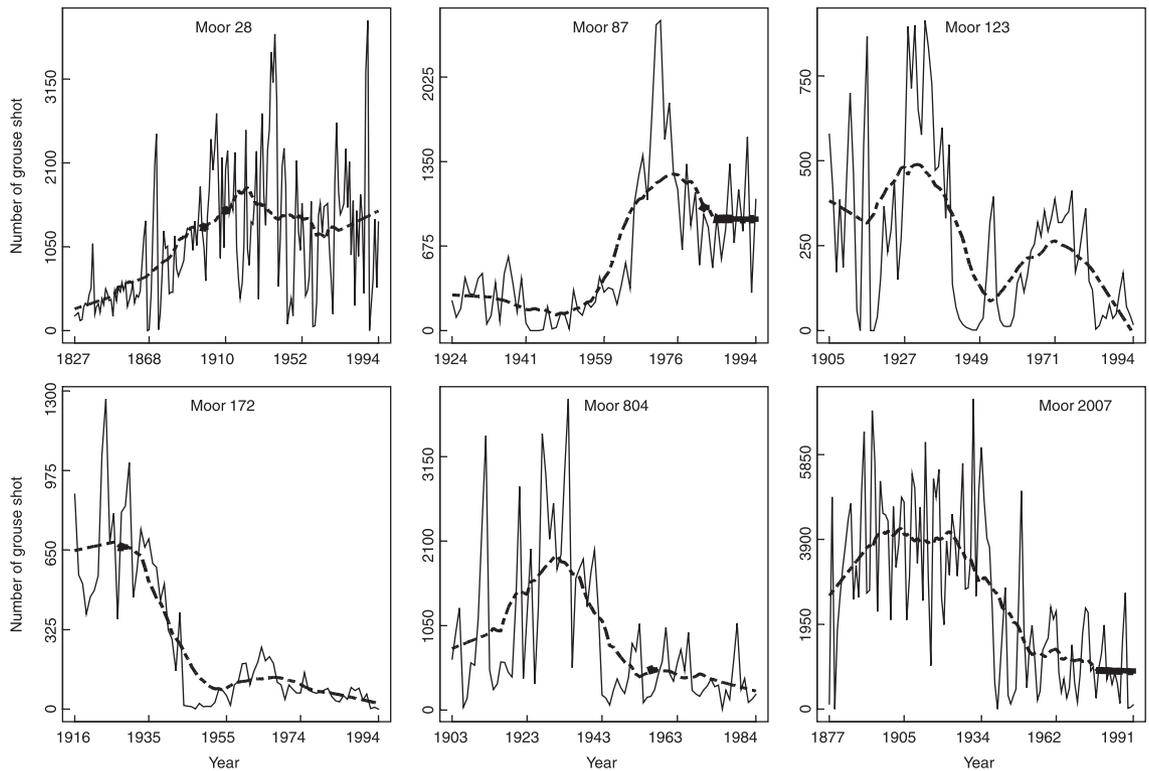
Fig. 1. (a–f) Examples of red grouse bag time-series showing the non-stationarity of the data, particularly around the Second World War. For each figure the solid line represents the raw time-series and the dashed line the smoothed time-series.
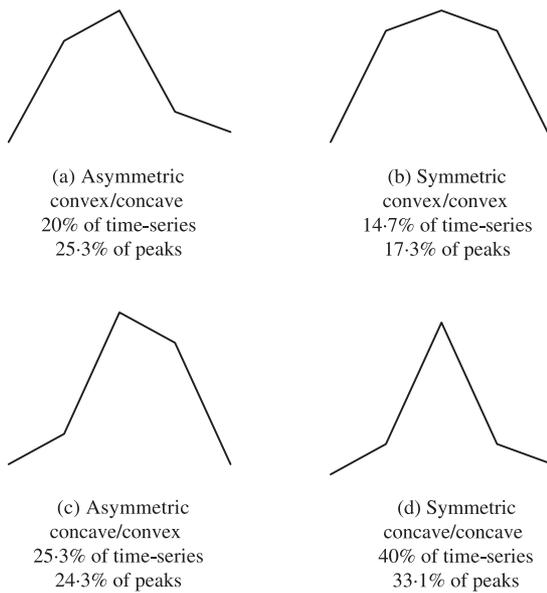

Fig. 2. Four possible peak shapes defined by the approach to and departure from peak density. (a) Asymmetrical, convex-up concave-down; (b) symmetrical, convex-up convex-down; (c) asymmetrical, concave-up convex-down; (d) symmetrical, concave-up concave-down. The first figure below each diagram indicates the percentage of time-series in which the indicated shape predominates, the second figure indicates the fraction of all peaks across all time-series of the indicated shape.

provided maximum growth rates consistent with observed maximum clutch size and juvenile survival (Hudson 1992), suggesting that the 25% tails of this distribution contained artificially extreme values caused

presumably by variation in the shooting effort per unit grouse density. Observed patterns of variation between rates on different moors was insensitive to the precise choice of percentile (results not shown). Growth and decline rates were Box–Cox transformed (lambda = −1·67 and 1·49, respectively) to normalize the data.

Density

Mean density of each population was estimated by dividing the average shooting bag by the area (km^2) of the moor obtained from surveys conducted in the late-1980s. Density data were normalized using a Box–Cox transformation, where lambda = 0·29.

TAR MODELS AND NON-LINEARITY

To investigate non-linear dynamics in red grouse time-series we looked for non-linearities that could be modelled using a threshold autoregressive (TAR) approach because of their broadly reasonable ecological structure and well-known statistical properties (Tong 1993; Hansen 1999). A TAR model takes the form:

$$x_t = b_0^{(1)} + \sum_{i=1}^{p_1} b_i^{(1)} x_{t-i} + \varepsilon_t^{(1)} \quad \text{if} \quad x_{t-d} \le r$$

$$\text{(eqn 1a,b)}$$

$$x_t = b_0^{(2)} + \sum_{i=1}^{p_2} b_i^{(2)} x_{t-i} + \varepsilon_t^{(2)} \quad \text{if} \quad x_{t-d} > r$$

denoted by TAR(d, p_1, p_2, r). We considered TAR models with one threshold, that could be located between

any one of the data points in the time-series, a lag value, d, of up to $\max(p_1, p_2)$ years, and AR models on either side of the threshold up to 3rd-order, thus the most complex possible model would be TAR(3, 3, 3, r). Model selection was that which minimized the NAIC. Having identified the best-fitting TAR model we performed a likelihood ratio test for non-linearity (the LM test – Moeanaddin & Tong 1988; as implemented in STAR, Tong 1993). The LM test examines the null hypothesis that $b_i^{(1)} = b_i^{(2)}$ ($i = 0 \ldots \max(p_1, p_2)$) using the ratio of the variance of residuals from the best-fitting TAR model ($\hat{\sigma}^2_{TAR,r}$) to the variance of residuals from the best-fitting AR model ($\hat{\sigma}^2_{AR}$) as a test statistic. Time-series were categorized as non-linear or linear depending on whether the null hypothesis was rejected ($b_i^{(1)} \neq b_i^{(2)}$) at the 5% level or not.

ENVIRONMENTAL VARIABLES

The number of days per year on which ≥ 1 mm of rain fell, averaged from 1960 to 1990, were obtained from 49 UK meteorological office weather stations (www.met-office.gov.uk). Station data were interpolated to produce a grid of the United Kingdom at a resolution of 1 km from which the number of rain days was estimated for each moor. Average total rainfall was interpolated in the same way. For 191/223 moors data on altitude (m), whether blanket bog was present, a measure of heather productivity, length of heather growing season (Hudson 1992), average yearly temperature and average temperature for the growing season (April–August) were available. Data on log transformed keeper density in the 1980s was present for 164 moors, and an estimate of underlying rock grade (see Hudson 1992 for description) was available for 108 moors.

STATISTICAL ANALYSES

Associations between time reversibility, GI ratio, linearity, ratio of symmetrical to asymmetrical peaks and cyclic behaviour were evaluated using χ^2 tests. For the rest of the analyses a combination of univariate and multivariate analyses were used. First, explanatory variables that had significant relationships with (i) measures of asymmetry (time reversibility, GI ratio, linearity); (ii) growth (density, growth and decline rates); and (iii) propensity to cycle and periodicity were identified. These were then placed into multivariate analyses and explanatory variables were added in the following order – artefactual (length of time-series), physical (e.g. easting) and biological (e.g. density). For binary variables (e.g. whether a time-series was time-reversible or not), generalized linear models with binomial errors were used. For measures of growth, density and cycle periodicity, analyses of variance and linear regression were used. The multivariate results reported are the test statistics, degrees of freedom (for $\chi^2 = 1$, unless stated otherwise) and P-values observed. Finally, to analyse whether regional proportions of the different

cycle shapes could be explained by regionally averaged environmental variables MANOVA was used. In all cases a $P < 0.05$ was taken to indicate significance.

Results

DATA TREATMENT

Normalization required that the data be approximately square rooted (the average Box–Cox exponent was 0·65 (range 0·34–0·99). Excluding 78 time-series that were indistinguishable from white noise, three that were AR-0 processes, and taking the longest time-series from nine populations with more than one non-white noise, non-AR-0 time-series resulted in a final data set of 223 time-series, all of which were ≥ 32 years in length (average length was 74 years, the median 72). There was a significant association between time-series length and region ($F_{19,203} = 2.201$, $P < 0.004$), with regions 5 (Moray) and 19 (Peaks) having proportionally longer and shorter time-series. No significant pattern was found between time-series length and either easting or northing ($t_{221} < 0.876$, $P > 0.382$).

MEASURES OF ASYMMETRY

Forty-four per cent (98/223) of the time-series were non-time-reversible. Average GI ratio was 1·24 : 1, indicating that grouse time-series spent almost 25% more time increasing in density than decreasing. While 80% of time-series spent more time increasing than decreasing (compared to 50% expected if no pattern) only 32% (71/223) of the GI ratios were significantly in excess of unity, indicating limited statistical power to detect asymmetry in individual time-series of these lengths. The average GI ratio for these 71 time-series was 1·47. Forty-four per cent (98/223) of the time-series failed the likelihood ratio test for linearity.

There was a significant association between non-time-reversible time-series and time-series with GI ratios significantly in excess of unity ($\chi^2 = 7.970$, $P < 0.005$). Non-linear time-series were 1·7 times more likely to be non-time-reversible than time-reversible ($\chi^2 = 12.344$, $P < 0.001$). The fraction of convex (increase)–convex (decline), convex–concave, concave–convex and concave–concave peak shapes was 18·3%, 25·3, 24·3% and 33·1%, respectively. Variation in this proportion was not associated with any other measure of asymmetry ($\chi^2_3 < 1.672$, $P > 0.643$).

ASSOCIATIONS OF ASYMMETRY AND OTHER VARIABLES

Locations of moors with time-series that were time/non-time-reversible and linear/non-linear, are shown in Fig. 3a,b. There were no significant relationships between occurrence of either time-reversibility or non-linearity with location, by which we mean easting, northing and their interaction ($\chi^2 < 1.179$, $P > 0.277$).

Fig. 3. Locations of time-reversible and non-linear time-series. (a) Rothman's time-reversibility test (filled circles indicate the location of moors with time-series that failed this test and were therefore deemed non-time-reversible); (b) the likelihood ratio test for non-linearity (filled circles indicate the location of moors with time-series that failed this test and were therefore deemed to be non-linear).

There were also no significant relationships between either time-reversibility or non-linearity and region ($\chi^2_{19} < 29 \cdot 213$, $P > 0 \cdot 062$; Fig. 4a,b). However, there was an increasing proportion of convex–convex symmetrical peaks in more easterly regions ($F_{1,18} = 12 \cdot 219$, $P < 0 \cdot 003$), but not in more northerly regions ($F_{1,18} = 1 \cdot 752$, $P = 0 \cdot 202$). There was no significant relationship between time-series with GI ratios significantly in excess of unity and location ($\chi^2 < 0 \cdot 631$, $P > 0 \cdot 426$). While there was a significant univariate relationship between time-series with GI ratios significantly in excess of unity and region, this effect disappeared if time-series length was added to the model first ($\chi^2_{19} = 26 \cdot 132$, $P < 0 \cdot 127$).

No measure of grouse moor environmental variability (rainfall, raindays or total), temperature (yearly average or heather growing season average), heather growing season length, or heather production was significantly associated with variation in measures of asymmetry ($\chi^2 < 1 \cdot 719$, $P > 0 \cdot 189$). Only three other variables emerged from the multivariate analyses as having a significant relationship with any measures of asymmetry: significantly shorter time-series and higher moor altitude with time-reversible time-series ($\chi^2 > 3 \cdot 934$, $P < 0 \cdot 047$); and decline rates with time-series with GI ratios significantly in excess of unity ($\chi^2 = 20 \cdot 575$, $P < 0 \cdot 001$).

DENSITIES

There was significant variation in mean densities between regions ($F_{19,195} = 3 \cdot 442$, $P < 0 \cdot 001$), even after account-ing for the significant univariate positive relationships with time-series length and location ($| t_{216} | > 3 \cdot 023$, $P < 0 \cdot 003$, with $R^2 = 0 \cdot 543$ for the full model). Regions 1 (Caithness and Sutherland), 8 (Cairngorm) and 13 (Lammermuir, Peebles, Pentlands and Moorfoots) had significantly lower residual mean densities, and regions 3 (Argyll, Cunninghume and Islay), 5 (Moray), 9 (Atholl) and 16 (North York Moors) had significantly higher residual mean densities (Fig. 4c).

Other parameters [area, rainfall (days and total), average temperature (April–August and yearly), presence of blanket bog, keeper density from the 1980s, heather productivity, length of growing season and rock grade] had significant univariate relationships with density ($| t | > 3 \cdot 53$, $P < 0 \cdot 001$). However, the most parsimonious multivariate model was obtained with time-series length, northing, keeper density from the 1980s, heather productivity and length of growing season ($| t | > 2 \cdot 486$, $P < 0 \cdot 014$, with $R^2 = 0 \cdot 542$ for the full model). Average density increased with keeper density and heather productivity but decreased with length of growing season.

GROWTH AND DECLINE RATES

Whereas growth and decline rates were significantly correlated with each other ($r = -0 \cdot 709$, $P < 0 \cdot 001$), no such correlations existed between density and growth/decline rates ($| r | < 0 \cdot 099$, $P > 0 \cdot 144$). There was significant variation in growth rates between regions
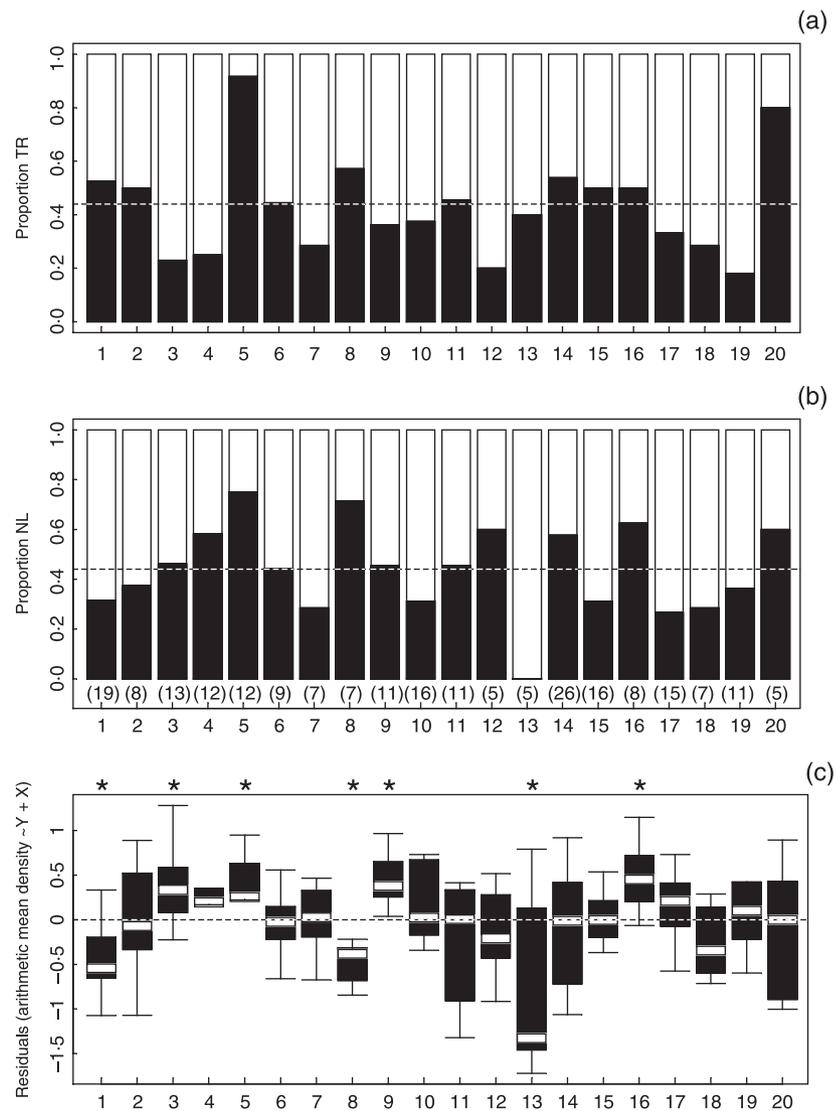
Fig. 4. Regional variation in (a) proportion of time-series that were non-time-reversible because they failed Rothman's test. (b) Proportion of time-series that were non-linear because they failed the likelihood-ratio test. The dashed lines indicate the regional average. (c) Residual mean density after accounting for variation with easting and northing. Sample sizes in each region are indicated in brackets. In (c) white bars correspond to the median for each region, black bars the interquartile range and the whiskers the regional range. Asterisks indicate deviation from the overall mean at the 5% level (see text). Regions are 1 = Caithness and Sutherland; 2 = East Ross, West Ross and West Highlands; 3 = Argyll, Cunninghame and Islay; 4 = Monadhliath; 5 = Moray; 6 = Buchan and Donside; 7 = Breadalbane, Rannoch and Tummel; 8 = Cairngorm; 9 = Atholl; 10 = Angus and South Deeside; 11 = South Tayside; 12 = Trossachs; 13 = Lammermuir, Peebles, Pentlands and Moorfoots; 14 = Borders, Dumfries and Galloway, Lowther and Northumberland; 15 = North Dales; 16 = North York Moors; 17 = South Dales; 18 = Bowland; 19 = Peaks; 20 = Wales.

($F_{19,201} = 2·497$, $P < 0·001$), even after accounting for the significant relationships with location ($|t_{221}| < 2·226$, $P < 0·027$, $R^2 < 0·022$). Regions 16 (North York Moors) and 20 (Wales) had significantly lower residual growth rates, and region 17 (South Dales) had significantly higher residual growth rates. Average annual temperature was also significantly associated with variation in growth rates ($F_{1,176} = 4·011$, $P = 0·046$).

Variation in decline rates was also significantly associated with moor region ($F_{19,203} = 2·708$, $P < 0·001$). Regions 7 (Breadalbane, Rannoch and Tummel), 9 (Atholl) and 16 (North York Moors) had significantly slower decline rates and regions 15 (North Dales) and 17 (South Dales)

had significantly faster decline rates. Interestingly, work on the parasites in England has shown that the two Dales areas (15 and 17) suffer from high intensities of *T. tenuis* infection, whereas the North York moors (16) has significantly lower levels of infection (Hudson *et al.* 1985). Blanket bog present on a moor was associated with faster decline rates ($F_{1,175} = 4·994$, $P < 0·027$), even after the regional variation had been accounted for.

CYCLE PERIOD AND PROPENSITY TO CYCLE

There was no association between whether a time-series was classified as cyclic or not and any measure of

asymmetry ($\chi^2 < 1{\cdot}416$, $P > 0{\cdot}234$). Non-cycling populations tended to occur on moors at a higher altitude ($\chi^2 = 6{\cdot}682$, $P < 0{\cdot}010$), even after accounting for time-series length. There was a significant decline in periodicity with time-series length ($t_{189} = -2{\cdot}66$, $P < 0{\cdot}009$) – but this is probably a straightforward power argument – shorter periods will be more evident than long period cycles in time-series of equal length. After taking into account time-series length and the increase with moor northing ($t_{188} > 2{\cdot}61$, $P < 0{\cdot}010$), moors with a smaller decline rate had a significant tendency to cycle with longer period ($t_{187} = 4{\cdot}52$, $P < 0{\cdot}001$). A significantly negative relationship between period length and GI ratio ($t_{187} = -2{\cdot}538$, $P = 0{\cdot}012$) remained after time-series length and northing had been accounted for. Period length and growth rate were significantly negatively related ($t_{186} = -2{\cdot}781$, $P = 0{\cdot}006$) (as observed by Hudson *et al.* 2002) after time-series length, northing and GI ratio had been accounted for, with $R^2 = 0{\cdot}148$ with all four parameters included.

Discussion

Three main conclusions may be drawn from this analysis of the shape of red grouse cycles. First, cycles in the shooting-bag records of red grouse are generally asymmetrical. More than 80% of 223 time-series examined spent longer in the increase than the decrease phase (although only for 32% was this difference significant) and overall, grouse time-series spend 25% more time increasing in density than decreasing. This asymmetry renders almost half the time-series significantly non-time-reversible. Significant non-linear structure was identified in 44% of time-series, and non-linear time-series were 1·7 times as likely to be non-time-reversible as linear series.

Secondly, higher growth rates in the south and east of the red grouse distribution range are associated with cycles of lower period, and these shorter cycles tend to be more 'saw-toothed' in shape. Slower growth rates in the north results in longer period cycles exhibiting greater equality in the times spent in the increase and decrease phases of the cycle. However, we failed to identify any clear patterns in the locations of non-time-reversible or non-linear time-series over the distributional range of red grouse in the United Kingdom. The occurrence of non-time-reversible or non-linear time-series was not associated with rainfall, temperature, latitude, moor area, average density or rates of population growth or decline.

Finally, we found no significant relationships between whether, or with what period, populations cycle and their time-reversibility and/or non-linearity status. It is a central tenet of population ecology that increasing growth rates can lead to higher frequency oscillatory and increasingly apparent non-linear dynamics (for example discrete logistic growth (May 1976), or in autoregressive dynamics (Stenseth *et al.* 1998a). It therefore comes as no surprise that as growth rates increase

towards the south and east, the period of observed population cycles decreases, and these cycles are more 'saw-toothed' and less symmetrical than the longer period cycles that are more common further north. The cline in maximum growth rates observed provides an obvious explanation for any change in periodicity and cycle shape from south to north. However, it is interesting that this cline is not associated with the time-reversibility or linearity results. This is presumably a result of slight and uneven statistical power which acts to obscure the influence of what is itself only a weak relationship between location and growth rate – an effect that is not overcome despite the very large data set available.

Asymmetries identified in the shooting records of red grouse might be considered as artefacts of a non-linear relationship between shooting effort and grouse density. It has been suggested that shooting effort is often disproportionately high in high-density years and disproportionately low in low-density years (Lambin *et al.* 1999). There are three reasons for doubting that asymmetry is artefactual: (1) it is difficult to conceive how a non-linear relationship between shooting effort and grouse density would create lateral asymmetry *de novo*; (2) Cattadori *et al.* (2003) found a good relationship between density estimated by direct counting and bag records, and a very close correspondence in the density dependent structures of both bag and count data, suggesting the former is a good proxy for actual grouse density; and (3) results from this analysis are consistent with conclusions regarding symmetry reported for populations where asymmetry has been studied using count data (Moss & Watson 1991; Hudson 1992). Could our failure to detect any significant trends in the occurrence of asymmetry or non-linearity arise from a bias in the statistical power available? We found non-time-reversibility more likely to be detected in longer time-series; however, while there was variation in the length of time-series from some regions, there was no systematic relationship between length of time-series and location of moors. Furthermore, we found no relationship between time-reversibility and cycle period.

Existing longitudinal studies of *T. tenuis* infection and host abundance from a selection of contrasting populations across the geographical range of grouse populations are incomplete, although regional comparisons and comparisons with respect to management have identified that parasite intensities are greater where predator control is more intensive (Hudson *et al.* 1992) and where there are more than 160 days of rain (Hudson *et al.* 1985). There are good reasons for supposing that grouse infection intensities will correlate with the number of days on which rain occurs. This climatic variable is associated with the development of peat and a moist sphagnum layer which facilitates parasite transmission (Hudson *et al.* 1985; Hudson 1992; Moss *et al.* 1993; Saunders *et al.* 1999). There is also good evidence from these damp moors that infection

levels are also a function of grouse density at an earlier time period (Hudson *et al.* 1992). However, we found no relationships between asymmetry or non-linearity of time-series and number of rain days or mean density of grouse (nor their interactions) and therefore no evidence to support the notion that rates of parasitism might influence the degree of non-linearity or time-reversibility of grouse cycles.

Non-time-reversible data can only arise as a result of non-linear dynamics. However, non-linear dynamics can result in either time-reversible or non-time-reversible time-series. Thus the significant relationship between non-time-reversibility and non-linearity is expected, and that 42/98 non-linear time-series were time-reversible requires no special explanation. However, that 42/98 non-time-reversible series were also apparently linear indicates anomalies in one or both of the testing procedures. Testing for non-linearity is problematic: while linearity is a well-defined phenomenon, there are many different forms of non-linearity and one test is not likely to be equally effective at identifying all of these different forms. We chose to look for non-linearities that could be modelled using a TAR approach because (1) they have a broadly reasonable ecological structure; (2) they possess well-known statistical properties (Tong 1993; Hansen 1999) and have a history of use in the ecological (e.g. Stenseth *et al.* 1998b; Grenfell *et al.* 1998) and economic literature (reviewed in Potter 1999); and (3) alternative software exists with which to check our computer programs and outputs. We originally chose three criteria for identifying non-linear time-series: AIC values for TAR and AR models (Akaike 1974; Tong 1993), the CUSUM test (Petruccelli & Davies 1986) and the LM test, but as expected we found AIC always favoured the TAR models over the AR models, and as reported previously (Moeanaddin & Tong 1988), we found the CUSUM test to be underpowered compared to the LM test (results not shown). Our choice of the TR test was based on studies of the power of this test with the BDS test (see Rothman 1992) and the bi-spectrum test (Hinich 1982). Time-series that we identify as non-time-reversible, but linear, arise perhaps because of the differential power of these tests to pick up different manifestations of the 'signatures' in what we know are noisy and heterogeneous time-series (Hudson 1992; Haydon *et al.* 2002).

Just under half the time-series examined showed evidence of non-linearity and cycle asymmetry, so while there appears to be plenty of variation in the shape of grouse cycles, no association between cycle shape and location, density or rainfall could be identified. While it remains possible that different processes may give rise to these patterns, we find no evidence for variations in grouse cycle shape being due to dual explanations for two different 'types' of grouse cycle, generated by fundamentally different biological processes on different moors. The results found here are more consistent with the observed dynamics arising from minor variations on a common mechanism.

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