POPULATION FLUCTUATIONS IN RED GROUSE:
ANALYSIS OF BAG RECORDS AND A SIMULATION
MODEL

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SUMMARY

(1) A time-series analysis of numbers of red grouse (Lagopus lagopus) shot per annum
was carried out for fifty-two moors in northern England where data were available for at
least 20 consecutive years during the period 1870–1977. Correlograms were constructed
and auto-correlation coefficients were tested for statistical significance.

(2) In the most representative sub-sample of moors, 83% of the series had significant
negative coefficients at $T + 2$ or $T + 3$ years or both. A mathematical model was fitted to
the fluctuations to describe their quasi-cyclic nature and the average ‘cycle-length’ was
found to be $4.84 \pm 0.086$ years.

(3) Field observations and data from trials with captive grouse were combined to
construct a simulation model of a red grouse population; its main features were:

(a) An inverse logistic curve relating mean numbers of the parasitic nematode
Trichostrongylus tenuis in adult red grouse to their breeding success.
(b) T. tenuis accumulation by young red grouse to steady state levels. The numbers of
worms accumulated per bird varied according to a combined effect of the density of
grouse prior to the breeding season and the worm burden of these grouse.
(c) A logistic curve relating the proportion of grouse shot with the density of grouse
available.
(d) An annual survival rate of the non-shot population inversely proportional to the
density of old grouse.

(4) The simulation model successfully captured mean levels and other population
parameters. However, it only gave a good fit to observed fluctuation patterns when
stochastic elements were introduced to represent known effects of weather.

(5) The model showed that red grouse cycles could be caused by effects of T. tenuis
working together with stochastic elements and a time delay arising from the uptake of
worms.

INTRODUCTION

Since 1956, the population dynamics of red grouse [Lagopus lagopus (L.)] have been
intensively studied in north east Scotland and recent reviews of this work are available
(Watson & Moss 1980; Moss & Watson 1980). Generally, these authors have considered
that cycles occur in population density, much as they do in the conspecific willow grouse
and in other Tetraonidae (Watson & Moss 1979). However, population changes over long
Population fluctuations in red grouse

periods of time have not been quantified and, as these workers acknowledge, the causes of
the cycles are not clearly understood.

Some analysis of long-term variation in numbers of red grouse shot annually (i.e. the
bag) was carried out by Mackenzie (1952), but he investigated only a few moors and used
the crude technique of comparing the frequency of 'peak years'. The lack of a quantitative
study of the fluctuations in red grouse bags is surprising since appropriate statistical
techniques have been available for over 30 years (Moran 1952).

In this paper we use time-series analysis of red grouse bag records from extensive areas
of moorland in the north of England to determine the nature of the population fluctuations
which are present. Also, we use field and laboratory data to construct a simulation model
of a red grouse population which produces these annual fluctuations.

METHODS

Analysis of red grouse bag records

Sixty-three moor owners in the north of England each provided us with the numbers of
red grouse which had been shot and recorded annually in their game-books. The area of
the moors and changes in area were also given. Several moors were contiguous, but
separate ownership and different management policies meant that the data sets were
largely independent. The geographical distribution of the moors used in our analysis is
shown in Fig. 1

Like Bulmer (1974), we chose a method of time-series analysis which was used by
Moran (1952) and more recently explained very simply by Poole (1974). This method
correlates the number of grouse shot in each year with the number shot in each succeeding
year at increasing time intervals. In a cyclic series, high correlations occur when the
intervals in years match corresponding phases of the cycle. For example, in a time-series
which peaks every 4 years, high positive correlations will occur at 4, 8, 12, 16 . . . years
with correlations of similar strength, but negative, at 2, 6, 10, 14 . . . years. The
correlations for each time-series are known as serial auto-correlations and are brought
together in a correlogram.

A little over half of the time-series showed long-term trends, usually down, which were
not relevant to our study of short-term fluctuations. These changes were often related to
the long-term reduction in area of heather—Calluna vulgaris (L.)—caused by the grazing
pressure of increasing numbers of sheep (e.g. Anderson & Yalden 1981) and since the
1950's, to reafforestation and reclamation of moors (Parry, Bruce & Harkness 1981). To
remove these trends, we smoothed the time-series and then subtracted the smooth curve
from the original values. The smoothed values were calculated by taking a 5-year moving
average which was itself averaged to produce an even smoother series. We repeated this
procedure ten times to produce a series good enough to subtract from the original data.
The 5-year average obviously could not be calculated for the first two and last two values;
so to avoid losing these points each time, we extrapolated two extra points linearly from
the two adjacent values.

There were a few short gaps in some of the bag records, mostly during war-time, but
these occupied less than 3% of the series and we considered it reasonable to interpolate the
missing points.

We did not construct correlograms for the eleven data series of less than 20 years in
length and auto-correlation coefficients were not calculated for intervals greater than
one-third of the length of the data series. This was so that correlated pairs of years would
not be associated with either end of the series, as would occur if large intervals were used on short series. Also we did not use grouse bags for years before 1870, thus we excluded the era when birds were 'walked up', rather than 'driven' over a line of standing guns.

Once correlograms had been constructed, we estimated the statistical significance of the auto-correlation coefficients by calculating confidence limits known as 'large-lag errors' (Box & Jenkins 1970). Two large-lag errors above and below the base-line of the correlogram give approximately 95% confidence limits. Values outside this confidence belt in either direction were considered to be significant.

**Inputs to simulation model**

**Red grouse numbers**

Accurate methods of finding red grouse with the help of trained dogs and of censusing prescribed sample plots of moorland, are well established (Jenkins, Watson & Miller **G. R. Potts, S. C. Tapper and P. J. Hudson**

FIG. 1. Locations of moors which had sufficient bag records for time-series analysis (○); study areas where T. tenus infestations were also measured (●). Moorhouse N.N.R. (M) and the main study area, which includes three moors (G). Stippled area shows land above an altitude of 300 m.
1963). The most important counts are those which estimate breeding density, usually in late March or early April and those which measure the season's production of fledged young, usually in mid-July.

With the initial help of David Jenkins of the Institute of Terrestrial Ecology at Banchory, both spring and August counts were started at Moorhouse National Nature Reserve (located on the map, Fig. 1) in 1961 and then carried out annually to 1981 (Taylor & Rawes 1974; Rawes 1976 et seq). During this period there was no shooting of grouse on the Reserve but our analysis of the bag records given by Taylor and Rawes for the period from 1908 to 1942 showed it then had a typical series of fluctuations: the reserve contains about 17 km² of grouse moor. Jenkins, Watson & Miller (1963) found over a 4-year period that the mean survival rate of adult grouse from March (the first count) to August (the second count) was 0.81. We have assumed this in estimating August population densities from March counts and have used the Moorhouse data to calculate overwinter survival in the absence of shooting.

In July or early August, estimates of the young:old ratio were made for eighteen moors where young and old grouse were counted by walking transects on 200 acre (0.81 km²) plots.

At twenty moors, counts of grouse were made as they were driven over the guns to determine the proportion which were shot. With the exception of our main study moors, we did not determine the population density of birds prior to shooting.

Parasitism: numbers of the nematode Trichostrongylus tenuis Eberth. in red grouse

Trichostrongylus tenuis is a parasitic nematode living in the caeca of red grouse. There are no intermediate hosts, the life-cycle cannot be completed in grouse and the many eggs are passed out of the host in the caecal faeces. After hatching and completing two moults on the moor, the (third stage) larvae make their way onto heather plants, thus infecting grouse food and completing the cycle.

We collected caeca from grouse shot during typical drives at seven moors in 1979, and at these moors and a further eight in 1980 and 1981. From 1975 to 1981, caeca were collected from grouse shot in both spring and autumn on moor 'G' (see map, Fig. 1). Grouse were separated into 'young' or 'old', according to the methods of Watson & Miller (1976) and sexed by dissection.

Caecal contents were washed with water over a 210 μm gauze. The adult worms were washed from the gauze, mixed with 300 ml of water and sub-sampled to estimate worm burdens per bird using the methods of Wilson (1979). Like Wilson, we found that the frequency distribution of worms per bird often did not conform to the negative binomial frequently found with parasite burdens. We found distributions were log-normal so we have used geometric means for average worm burdens throughout. We have assumed that worm burdens in shot grouse were similar to those in grouse which were not shot. Post-mortem examinations were carried out on grouse found dead on our study areas.

RESULTS

Annual fluctuations in red grouse bags

We found that only two out of sixty-eight statistically significant auto-correlation coefficients had a time interval greater than 5 years; showing that the correlograms were 'damped'. We tested this conclusion by comparing the frequency distribution of significant coefficients to an expected random distribution based on the number of auto-correlations
performed for each time interval. The expected frequencies were calculated by summing the number of auto-correlation coefficients that had been computed for all series within each time interval and distributing the total number of significant coefficients found (68) between the time intervals in proportion to the number actually calculated. Some series were too short to allow calculation of the 9- and 10-year time intervals. The two distributions were significantly different (Table 1). All the significant auto-correlation coefficients at a time interval of 1 year were positive and all others were negative.

<table>
<thead>
<tr>
<th>Time interval (years)</th>
<th>Observed</th>
<th>Expected per interval</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>9</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>68</td>
<td>68</td>
</tr>
</tbody>
</table>

The two distributions are significantly different (G-test: \( P < 0.005 \), note time-series of less than 20 years excluded.

In truly cyclic species (‘phase remembering quasi-cycles’—Nisbet & Gurney 1982), such as the Canadian lynx (\( L. c. c. \) Kerr), significant positive and negative correlation coefficients occur at each cycle and half-cycle for up to 30 years, with little or no damping (Moran 1953; Poole 1974), but the correlograms for the red grouse were so damped that usually only the first half-cycle was significantly above noise level. We have therefore concluded that these series do not exhibit true cycles, but are what Nisbet & Gurney (1982) term ‘phase forgetting quasi-cycles’. Thirty (58%) of the time-series were of this type, that is to say they had significant negative coefficients at time intervals of 2 or 3 years, or both. This proportion rises to 83% when the small moors (<8 km\(^2\)) and relatively short series (<50 years) are excluded.

An auto-regression equation was then fitted to the series to represent the quasi-cycles. Since the correlograms we observed were damped, we considered that this simple auto-regression format would suffice. The following equation was therefore fitted to all detrended series, where \( X = \) the number of grouse shot and \( T = \) the year:

\[
X_T = aX_{T-1} - bX_{T-2} + \epsilon_T.
\]

Poole (1974) showed that adding a third or fourth term to the auto-regression equation makes little difference to such models and our equation was accordingly limited to the two coefficients. Using the above equation, we then generated a model correlogram. Figure 2 gives the results of the analysis for two typical contrasting types of moor, one which showed significant quasi-cycles (Fig. 2(a)) and one which did not (Fig. 2(b)).
Fig. 2. Procedure for analysis of serial correlations in red grouse bag records and comparison of correlogram outputs for a typical quasi-cyclic moor (Fig. 2(a) left) and a non-quasi-cyclic moor (Fig. 2(b) right). From the top in each case, the original bag data are given (i) and the detrended series (ii). Bottom left (iii) are correlograms indicating the two significant negative coefficients of the quasi-cyclic moor and the lack of these in the non-quasi-cyclic moors. The auto-regression model correlograms are given as Fig. 2(a) (iv) where $X_t = 0.32X_{t-1} - 0.30X_{t-2}$ and in Fig. 2(b) (iv) which had no significant negative coefficients.
To obtain a measure of cycle length, we calculated the auto-regressive period. From the above equation it follows that:

\[ X_T - aX_{T-1} + bX_{T-2} = \varepsilon_T. \]

We then used the following equation to calculate cycle length after Kendall (1946):

\[
\text{Cycle length} = \frac{2\pi}{\cos^{-1} \left( \frac{a}{2\sqrt{b}} \right)}.
\]

Of the thirty moors which showed evidence of quasi-cyclic fluctuations, 80% had average ‘cycle-lengths’ between 4 and 5 years, and the average for all moors was 4.84 ± 0.086 years.

**Components of the simulation model**

**Breeding success**

Trials with red grouse in captivity have demonstrated that infection with *T. tenuis* causes anaemia, hypoproteinaemia, lower egg production and, at high levels, death (Wilson & Wilson 1978). We therefore compared worm burdens in old grouse shot in August with breeding success in the same year, for each of the moors in our field studies.

In both 1979 and 1980 we found that breeding success, measured as young:old ratio on the moor (=R), decreased with geometric mean worm burden (=W) (Fig. 3). There was no notable difference between the 2 years, the equation being:

\[
R = 3.40 - \left[ \frac{3.40}{1 + \exp \left( 2.217 - 0.000464W_T \right)} \right].
\]  

(1)

![Fig. 3](image-url) Inverse correlation between young:old ratio of red grouse in August on moors [(●) Fig. 1] and geometric mean number of *T. tenuis* worms in the old birds. Data from 1979 (indicated), and 1980 were similar and are combined; the mean worm burden in adult grouse found dead (N = 32) is indicated by the symbol (†).
Population fluctuations in red grouse

The asymptote, 3.40 in the above logistic [the curve giving the best fit and which explains 40% of the variation in R (P < 0.001)], is close to the maximum ratio we have recorded, indeed it is near the maximum expected. With no nest losses and 100% chick survival, R would be 3.7.

There are two lines of reasoning which also support the general form of eqn (1). First it is clear from several studies that deaths begin to occur at levels of worm burden which according to eqn (1), greatly lower breeding success. For example, the geometric mean worm burden of grouse which post-mortem showed had died of no apparent cause other than of T. tenuis infection was 5120 ± 173 on our main study moor. In our case, the geometric mean worm burdens in dead birds dying of T. tenuis infection was 0.88, the arithmetic mean. Using 0.88 to correct the arithmetic means of other workers, our estimate compares with 5245 from the Glen Esk moors (Jenkins, Watson & Miller 1963) and 5916 in trials with captive birds (Wilson & Wilson 1978), but is lower than the 6898 reported by Cobbett & Graham-Smith (1910). Some less heavily parasitized birds may breed successfully on a moor whilst others are dying (e.g., see Fig. 3) which may account for the decreased slope in the effect of worm burdens, so that R, in eqn (1) is not reduced to zero until a mean worm burden in excess of that found in the dead birds.

Second, the slope in eqn (1) is similar to that for egg production in captive birds studied by Wilson (1979), if his measure of infection (T. tenuis eggs per gram of caecal faeces) is converted to worm burdens.

Trichostrongylus tenuis numbers in red grouse

We found that worm numbers (= W) increased rapidly through August and September in young grouse on all moors.

Between moors, the overall uptake of worms in young grouse by 1 September (the average date of shooting), appeared to vary in response to the density of infective larvae. Using data from the moors sampled in 1979 and 1980, multiple regression analysis showed that 64% of the variation in the geometric mean number of mature T. tenuis in young grouse on 1 September (= W1) could be accounted for, by the worm numbers in the old grouse (W2) and the bag km⁻² in the previous autumn (B$_{T-1}$): W1 = 72.85 [W$_{T}$·B$_{T-1}$/1000]$^{0.375}$, ($r^2 = 0.64$, $P < 0.001$), see Fig. 4. There was no correlation with bag 2 years previously or with that in the year when breeding success was measured.

A high bag is normally followed by a high density of grouse in the next breeding season (see later), but we did not know exactly when grouse density was responsible for increasing worm burdens in young grouse.

Next we dealt with uptake of worms after 1 September. Within each of the 3 years 1979–1981 combined, worm numbers (W) could be estimated from the number of days after 20 July (= D) by the equation W = 12.19D ($r^2 = 0.87$, $P < 0.001$). Later in autumn, the uptake of worms is likely to slow and then cease when the mean temperature drops below 6 °C, the minimum needed for hatching of the eggs and larval survival (Michel 1969). The date when uptake ceases is thus likely to vary from year to year but would on average be about 1 November. Allowing 10 days for maturation in the host, the over-winter worm number, i.e. that from 10 November onwards, will amount to 2.7 times the level achieved on 1 September.

After allowing for the effects of varying challenge arising from density of grouse and worm numbers in old grouse on our main study area, the uptake in 1978 was 4.54, the expected value ($P < 0.05$) and in 1981, 0.37 of expected (P. Hudson unpublished). We therefore incorporated a stochastic term s to include these effects with a mean value of 2 [(4.54 + 0.37)/2].
The number of worms acquired by the young in their first autumn (= \(W_2\)) is now calculated:

\[
W_2 = 2.7 \times 10^{3} \left[ W_T \cdot B_{T-1}/1000 \right]^{0.375}. \tag{2}
\]

Worm numbers in old grouse shot in August after breeding were not significantly different from grouse shot earlier in mid-April before breeding and there was no significant increase in worm burdens in old grouse in late summer and early autumn. These observations indicate that a ‘steady state’ in worm numbers is reached during the first autumn of life. The strong immuno-suppression system observed by Wilson & Wilson (1978) presumably provides the mechanism maintaining the ‘steady state’, the initial uptake then being attributable to the less developed system in young birds.

It follows from eqn (2) that the worm burdens in breeding grouse (\(W\)) in the year \((T + 1)\) can be estimated:

\[
W_{T+1} = (W_T \cdot N_T + W_2 \cdot Y_T)/N_T + Y_T, \tag{3}
\]

where \(N\) are old grouse and \(Y\) young grouse.

**Shooting**

Grouse shooting on our study areas comprised drives of birds from areas of 1–1.5 km\(^2\); the methods are similar to those for the grey partridge \(\text{[Perdix perdix (L.)]}\) where the number of shooting days is adjusted to density, since it is impractical to ‘drive’ where densities of birds are lower than 80 km\(^{-2}\). For both partridges and grouse we have clear evidence that the proportion shot increases with density in a way described by a logistic curve. At high densities they become more wary as a result of repeated driving. We have
used the equation given by Potts (1980) which best fitted the red grouse data, where the bag (=\( B \)) is the number shot and \( A \) is the density of adults and young on 1st August:

\[
B = A \left[ \frac{0.55}{1 + \exp \left( 5.7 - 0.04A \right)} \right].
\]  \hspace{1cm} (4)

**Survival from 1 year to the next**

Breeding densities and production data for Moorhouse are summarized in Table 2 column 1 for a 20-year period, during which there was no shooting. Mean annual survival rate from 1st August was 0.37 ± 0.04. Annual variation in overall survival from 1st August (=\( S \)) was inversely related to the density of old birds present on 1st August (=\( N \)), though in the model, \(-N\) where appropriate:

\[
S = 1.002 - 0.377 \log_{10}(N - B),
\]  \hspace{1cm} (5)

\[ (r^2 = 0.44, P < 0.01) \text{ S.E. of slope } \pm 0.013. \]

Below densities of 10 km\(^{-2}\), i.e. outside the range of Moorhouse data, \( S \) was set at 0.62 (see Fig. 5).

In a series of removal experiments, Watson & Jenkins (1968) provide an explanation for our observations described by eqn (5). Resident old grouse prevented some young from taking territories; when removed by shooting, the old birds were replaced by young non-territorial birds.

![The annual survival of red grouse at Moorhouse N.N.R. from 1 August compared with the density of adult grouse present.](image)

**The simulation model**

The equations for calculating red grouse breeding success, grouse survival and \( T. tenuis \) burdens were assembled in sequence according to the flow diagram of the simulation model outlined in Fig. 6. Our aim has been to keep the model as simple as possible and to investigate serial correlation in bags.
Fig. 6. Flow diagram relating equations used in the computer model which simulated quasi-cycles in red grouse bags (number shot) in northern England. Continuous lines represent grouse numbers, broken lines refer to the worm sub-routine. Lines represent year T, delays into following years being indicated.

Our model [particularly eqn (1)] assumes that grouse predators were kept under control by gamekeepers and that predation was not an important cause of loss. Also our data is limited, being based on a mixture of information from shot moors where heather is managed, i.e. burnt (as described in Miller & Watson 1978) and an unshot moor (Moorhouse), where heather is not managed. It follows that until better data are available, the model cannot be used to evaluate heather management, which would affect the slope of density dependence in eqn (5). Moreover, in eqn (2) worm burdens are a function of grouse shot. As already explained, this does not affect the simulations as used in this paper but it does prevent use of the model to explore the effects of variations in shooting on levels of parasitism.

The model was initiated with two numbers; old grouse km$^{-2}$ on 1st August and number of worms per bird. In the first simulation run, none of the variables were stochastic, the only inputs being the two model initiators. Within 7 years, this deterministic simulation came to realistic equilibrium levels in all output parameters (Table 2 column 5).

Sensitivity analysis

Next we carried out sensitivity analysis by changing and omitting variables one at a time in order to measure the relative importance of the components to the simulation output. We concentrated our attention on the causes of the quasi-cycles.

(1) Deterministic simulations

There was no sign of quasi-cycles in bags in deterministic simulations, no matter how much the initiators were varied, but the outputs gave realistic equilibrium levels (e.g. compare columns one, two and five in Table 2). Levels were determined by the interaction
### Table 2. Estimates of population statistics for red grouse in Northern England in a comparison of moors and computer simulations

<table>
<thead>
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</tr>
</thead>
<tbody>
<tr>
<td><strong>Density of pairs in April</strong></td>
<td>35·64 ± 5·16 km⁻²</td>
<td>36·68 ± 4·91†</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Density of old on 1 August (km⁻²)</strong></td>
<td>58*</td>
<td>42 ± 5·46</td>
<td>45</td>
<td>65</td>
<td>46</td>
</tr>
<tr>
<td><strong>Young:old on 1 August</strong></td>
<td>2·00</td>
<td>2·30</td>
<td>2·49</td>
<td>2·03</td>
<td>2·54</td>
</tr>
<tr>
<td><strong>± S.D. of young:old ratio</strong></td>
<td>±0·94</td>
<td>±0·91</td>
<td>±0·46</td>
<td>±0·48</td>
<td></td>
</tr>
<tr>
<td><strong>Density of young and old on 1 August (km⁻²)</strong></td>
<td>169</td>
<td>140</td>
<td>158</td>
<td>208</td>
<td>162</td>
</tr>
<tr>
<td><strong>Bag (km⁻²)</strong></td>
<td>55‡</td>
<td>50§</td>
<td>57</td>
<td>0</td>
<td>62</td>
</tr>
<tr>
<td><strong>Mean worms in old in August</strong></td>
<td>2400†</td>
<td>2339</td>
<td>3229</td>
<td>2500</td>
<td></td>
</tr>
<tr>
<td><strong>Length of quasi-cycle (years)</strong></td>
<td>4·8</td>
<td>4·8**</td>
<td>4·5</td>
<td></td>
<td>none: complete damping in &lt;7 years</td>
</tr>
</tbody>
</table>

* Assuming constant survival of 0·81 from April to August (see text p. 24 though data in † below suggest it may be lower in our studies).
† Five moors counted annually 1971–81 (David Jackson, Game Conservancy in litt).
‡ Between 1908 and 1936.
§ All moors, Game Conservancy National Game Census 1961–81 (Tapper 1982).
ε 1976–81 only.
** See p. 77.

of the density-dependent factors and they were most sensitive to the density-dependent effects of old birds on recruitment as calculated from eqn (5).

(2) **Stochastic simulations**

Stochastic variation was first added to the young:old ratio, which took account of the variation around the inverse logistic curve relating young:old ratio to worm density (Fig. 3). The variance introduced was adjusted to approach that observed in young:old ratios (see Table 2). This was sufficient to generate and maintain weak quasi-cycles. Simulations were of significantly higher fidelity however when a further stochastic term was introduced to worm numbers by giving the term s in eqn (2) a variance of 0·7.

Outputs of simulated bags with both sources of stochasticity closely represented those observed on the moors, see Fig. 7(a) and produced a quasi-cycle with a period of 4·5 years (see third column Table 2). The auto-regression equation of the simulation used in Fig. 7(a)

\[ X_T = 0·21 X_{T-1} - 0·38 X_{T-2} \]

gives two significant negative coefficients and is well within the range observed on moors. When worm effects [eqn (3)] were removed from the model, the quasi-cycles disappeared; Fig. 7(b),

\[ X_T = 0·21 X_{T-1} - 0·11 X_{T-2}, \]

the negative term not being statistically significant \((P > 0·05)\). This showed that the time delay responsible for the quasi-cycles arose through the uptake of worms and the relation of this to the density of grouse.
Sensitivity analysis thus showed that the quasi-cycles had three essential features, effects of worms, stochastic variation, particularly on breeding success and a time delay arising from the uptake of worms.

The model not only represents and provides a hypothesis for the quasi-cycles; it is also compatible with the most important findings concerning red grouse numbers in the studies by Watson and co-workers in north-east Scotland. In particular, their findings on the roles of territorial behaviour and annual variation in heather quality are not inconsistent with our model. The effects of shooting on managed grouse populations are rather slight (Table 2) again in agreement with their findings.

**DISCUSSION**

We have shown that red grouse bags from moors in northern England fluctuated in a manner, which may be termed ‘phase forgetting quasi-cycles’ after Nisbet & Gurney (1982). We found no true cycles or ‘phase remembering quasi-cycles’. This finding has important practical considerations because it is not possible to predict accurately the timing of peaks and troughs in grouse numbers. However, we found that successive years were usually positively correlated and that intervals of 2 and 3 years gave significant negative correlations. There was therefore a significant tendency for periods of high numbers to be followed by periods of low numbers and we have considered the term ‘phase forgetting quasi-cycles’ to be appropriate.

Nisbet & Gurney (1982) suggest that ‘phase forgetting quasi-cycles’ may be generated in one of three ways. Firstly, a deterministically stable but under-damped system is driven by aperiodic external fluctuations—‘exogenous resonant quasi-cycles’; secondly, a similar deterministic system is disturbed by demographic stochasticity—‘exogenous resonant quasi-cycles’; or thirdly, a deterministic system which generates limit cycles but is perturbed by environmental or stochasticity—‘perturbed limit cycles’. We have strong evidence to suggest that the stochastic variation is exogenous since we found a high degree of synchrony between moors (Tapper 1983) indicating that separated populations were
being subjected to the same random effects. Our model is therefore built round a
deterministic system which is stable but is disturbed by stochastic variation acting on
variables known to be heavily influenced by weather. Moss, Watson & Parr (1975) found
that young:old ratios were a function of the density (g/m^2) of heather remaining in spring
from the previous summer’s production and the increment of nitrogen in heather prior to
clutch completion, both attributable to variations in the weather. Likewise it is clear that *T.
tenius* larvae are susceptible to dry or cold conditions on the moor (Committee of Inquiry
on Grouse Disease, 1911). The deterministic component is generated by the action of a
parasite acting as a delayed density-dependent factor.

Controversy has always surrounded the role of *T. tenius* in red grouse population
fluctuations. A grouse ‘disease’ was first attributed to ‘very small worms’ in 1854, but at
the same time was considered to be troublesome only when the heather was damaged by
frost or had become ‘unwholesome’ (MacDonald 1883). Nevertheless, the ‘disease’ was
also recognized to result from a high density of grouse 1 or 2 years earlier (Payne-Gallwey
1892). Food was stressed in the report of the Committee of Inquiry on Grouse Disease
(1911) and their case against *T. tenius*, argued mainly by Lord Lovat, rested on the fact
that some declines of red grouse populations were not accompanied by high levels of
parasitism.

Our model resolves these apparent contradictions because in the quasi-cyclic output,
there frequently were years when the effects of the parasite were dwarfed by the stochastic
elements.

The data provided by Jenkins, Watson & Miller (1963) are not readily comparable to
ours but they clearly show that mean grouse breeding success and mean grouse ‘condition’
were both lower in years when numbers of *T. tenius* were higher. However, it was also
found that some grouse in good condition had as many worms as some grouse in poor
condition and it was concluded, ‘clearly the number of worms was not the cause of
differences in condition, but perhaps a consequence’. The real cause was not determined,
but Watson & Moss (1979) suggest that ‘stress resulting from social behaviour predisposes
certain social classes to suffer more from such parasites’. By contrast our work indicates
that much of the parasite uptake occurs in August and September before the social stresses
which are involved in acquisition of the territories.

After 4 years—and a typical quasi-cycle—the work in north-east Scotland shifted to
Kerloch, where *T. tenius* was largely ignored (e.g. Watson & Moss 1980). We have carried
out a time-series analysis of the Kerloch bag records from 1920 to 1964 [given by Jenkins
& Watson (1970)] and they showed no significant quasi-cycles.

With hindsight, the main reason for the differing opinions on *T. tenius* seems to have
been that workers were expecting a single too-simple cause of population fluctuations. *T.
tenius* has, we believe, an essential but not overwhelming role to play in determining the
quasi-cyclic patterns of fluctuation; it is not the sole or even the major cause of them, but
without the parasite they could not occur.

The cycles exhibited by our data (*X = 4.8 years*) appear to be shorter than those
suggested for Scottish moors. Mackenzie (1952) examined the records of the Atholl estate
and suggested these showed a cyclical period of between 5.9 and 6.9 years. Watson &
Moss (1979) confirm that 6 years appears to be the length of cycle in Scottish red grouse
populations in recent years. It is not clear from our analysis what causes this fundamental
difference in cycle length between English populations and Scottish ones, two alternative
possibilities are that the time lag in the density-dependent mortality is shorter on English
moors than it is further north or that red grouse populations in England have a higher
reproductive output than Scottish populations. Either of these would produce shorter cycles.

Our conclusion of the importance of worms is out of line with recent findings (Anderson & May 1979; May & Anderson 1979) that microparasites such as viruses are more likely to regulate or control vertebrate population densities than macroparasites such as nematodes. However, looping-ill, the main virus which affects grouse (Duncan et al. 1978), was absent from our quasi-cyclic moors. Our conclusion is also out of line with general experience that parasites do not often affect bird population densities, but grous on managed moors exist at far higher densities than those on unmanaged moors so may be expected to have some characteristics of the domestic herbivores where densities are high and parasites important.

Our model based on field data, gives a possible explanation for the regularity in the fluctuations of red grouse in northern England; the explanation is simple and offers much scope for testing in the field, particularly for experiments which both increase and remove the parasite burdens.

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REFERENCES


Population fluctuations in red grouse


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