THE EFFECT OF A PARASITIC NEMATODE ON THE BREEDING PRODUCTION OF RED GROUSE

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SUMMARY

(1) The breeding success of female red grouse treated with an anthelmintic to reduce an infection of the nematode *Trichostrongylus tenius* was compared over a period of 3 years with that of a control group. Treatment significantly increased the production of young per female in all years.

(2) Breeding success showed a significant, negative correlation with parasite numbers in old grouse, both within and between areas (in 4 out of 5 years).

(3) The role of parasitic nematodes in the population cycles of red grouse are discussed in relation to current models and previous studies.

INTRODUCTION

Population studies on red grouse *Lagopus lagopus scoticus* (Lath.) have found that poor breeding success is often associated with high infections of the nematode, *Trichostrongylus tenius*, in the birds’ caeca (Jenkins, Watson & Miller 1963; Potts, Tapper & Hudson 1984). From field observations and the development of simulation (Potts, Tapper & Hudson 1984) and theoretical models (Hudson, Dobson & Newborn 1985), our work has suggested that parasitism may be an important factor causing the cyclic fluctuations in numbers of red grouse shot in the north of England.

To test whether infections of *T. tenius* reduce the breeding production of red grouse, an experiment was conducted on wild grouse. The breeding success of two groups of grouse was monitored: one control group with a natural infection and a second experimental group with an infection reduced through the effects of an anthelmintic. Field data were also collected from a number of areas to provide an analysis of breeding production and parasite levels within and between areas, so as to place the experiments in perspective.

METHODS

*Experimental reduction of parasite infection*

The experiment was conducted on a 50-ha area of managed grouse moor in upper Swaledale, North Yorkshire. In March 1982 and 1983 hen red grouse were dazzled at night with a quartz halogen lamp and caught with a large net. Hens were treated orally with 2 ml levamisole hydrochloride (Nilverm) to reduce the infection of *T. tenius* or were given 2 ml water as a control. The capture success rate was high and alternate birds were treated with the anthelmintic. Radio transmitters, supplied by Biotrak Ltd, were fitted to the back of each bird using an elastic harness looped around the base of each wing and across the sternum. Transmitters weighed 13.5 g, approximately 2% of body
weight; observations on radio-tagged and untagged hens, respectively, indicate that transmitters did not influence movements or behaviour more than 5 days after capture (see also Lance & Watson 1977; Angelstam 1984). Each transmitter was tuned to a specific frequency within the allotted band so that individual birds could be identified and located by their radio signal. When all available transmitters were in operation, additional birds were fitted with back tabs (after Furrer 1979; Green 1983), each with a unique colour combination and a harness similar to that used for the transmitters. Not all of the nests of colour-tagged birds were located during the breeding season, and in 1982 some of the transmitters stopped working prematurely; this accounts for differences in sample size between experimental and control groups.

In late 1983 the study area was increased to 800 ha in which hens were caught and treated as before. Capture of hens started in December and continued to mid-April 1984, but in this year only back tabs were fitted to hens.

Disturbance during nesting was kept to a minimum. Each hen was disturbed from the nest once during the latter half of incubation to count the number of eggs being incubated. No hens deserted as a result of this disturbance. Hatching date was determined by inspecting nests carefully with binoculars from a vantage point and taken as the day the hen left the nest with her brood. When chicks were 10 days old, hen grouse were located and their chicks found using a trained dog (pointer or setter). Chicks were tagged with small, numbered patagial tags, and records were kept of when these birds were recaught or shot. In 1984 brood size was not estimated until July, when broods were about 6 weeks of age.

As the experiment was designed to test whether the reduction in the level of infection improved breeding success, statistical tests for the experimental results are one-tailed. The effects of the anthelmintic on the infection of T. tenuis was checked in two ways. First, in 1982 and 1983 faecal samples were collected from radio-tagged birds. Roosting hens were located, after incubation, at night using an AVM LA12 receiver, and the caecal faeces containing the eggs of the parasite were collected on the following morning. Approximately 1 g of each sample was weighed and shaken in 20 ml of saturated salt solution; this was then subsampled and eggs of T. tenuis counted using the McMaster egg counting technique (Gordon & Whitlock 1939). Secondly, in 1983 and 1984 some of the tagged birds were shot after 12 August, the caeca were removed and the contents washed with water over 210 μm gauze. The adult worms were washed from the gauze, mixed with 300 ml of water and subsampled to estimate the number of worms per bird; mean values are expressed as geometric means (after Wilson 1983).

Comparison of breeding production and infection within an area

At a distance of 1 km from the experimental area, an 80-ha count area was established on which standardized counts were conducted each July as described by Jenkins, Watson & Miller (1963). The ratio of young to old birds seen in each year was taken as an estimate of breeding success.

All grouse shot from an area of 1700 ha, which included the count area and the experimental area, were inspected after each shoot. Birds were aged from plumage characteristics, claw scars and relative skull strengths (after Watson & Miller 1976) and guts from a sample of old birds removed for analysis. Grouse used in the experiment and subsequently shot were not used in this analysis. Levels of infection with T. tenuis were determined as described above.
Comparison of breeding production and infection between areas

Between 1979 and 1983 twenty-one grouse moors from the north of England were visited on shooting days in August and early September. Not every estate was visited in each year but the study concentrated on six estates in the central Pennines which readily provided access to birds and were visited in at least 3 of the 5 years. Shot birds were aged, gut samples taken and level of *T. tenuis* infection determined, as previously described. Few gut samples were taken in 1979 but only samples containing more than ten birds were used for analysis in other years.

In 1979 and 1980 the ratio of young to old birds shot was taken as an estimate of breeding production. In 1981, 1982 and 1983 counts were made in July and the ratio of young to old birds counted used as an estimate of breeding success.

RESULTS

The effects of reduced infection on grouse production

Counts of worm eggs in grouse faeces (2 months after treatment) and the number of worms per bird (5 months after treatment) showed lower levels of infection than in control birds (Table 1).

<table>
<thead>
<tr>
<th>Year</th>
<th>Infection</th>
<th>Treated birds</th>
<th>Control birds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean   S.E.  n</td>
<td>Mean   S.E.  n</td>
</tr>
<tr>
<td>1982</td>
<td>Eggs g⁻¹ faeces 2 months after treatment</td>
<td>5·0    2·6  4</td>
<td>87·1  2·4 9</td>
</tr>
<tr>
<td>1983</td>
<td>Eggs g⁻¹ faeces 2 months after treatment</td>
<td>72·1   1·4  7</td>
<td>223·4 1·4 8</td>
</tr>
<tr>
<td>1984</td>
<td>Worms per bird 5 months after treatment</td>
<td>2149  1·2  6</td>
<td>8996  1·1 7</td>
</tr>
<tr>
<td></td>
<td>Worms per bird 5 months after treatment</td>
<td>865   0·1  5</td>
<td>2032  0·1 20‡</td>
</tr>
</tbody>
</table>

† Significance determined from one-tailed *t* test where N.S. = not significant; * = *P* < 0·05; ** = *P* < 0·02; *** = *P* < 0·01.
‡ In 1984 there were no control birds so treated birds are compared with wild birds.

Treated hen grouse reared significantly more young than control birds (Table 2). The difference was most marked in 1983 when control birds had a high infection (Table 1). In 1982 there was no significant difference in clutch size between treated and control birds and only a tendency for hatching success to be greater (*P* < 0·1), although overall chick production was significantly greater (*P* < 0·05).

A number of tagged chicks were subsequently recaptured or shot over the following winter (Table 3) and there was no difference in the proportion tagged and recaptured from broods with treated and untreated hens, respectfully.

Comparisons of breeding production and infection within an area

Production of young grouse, taken as the ratio of young to old birds counted in July, decreased with the mean levels of *T. tenuis* burdens in old grouse (Fig. 1). The area was not shot in 1983, so the estimate of worm burdens was taken from the control birds in the experiment.
Parasites and grouse production

Table 2. Breeding production of hen grouse treated with an anthelmintic compared with control hens given water (not 1984). Figures shown mean with standard errors

<table>
<thead>
<tr>
<th>Year</th>
<th>Factors</th>
<th>Treated birds</th>
<th>Control birds</th>
<th>Significance†</th>
</tr>
</thead>
<tbody>
<tr>
<td>1982</td>
<td>Number of birds</td>
<td>8</td>
<td>14</td>
<td></td>
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<tr>
<td></td>
<td>Clutch size</td>
<td>8.25±0.62</td>
<td>7.93±0.36</td>
<td>N.S.</td>
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<td></td>
<td>Hatching success</td>
<td>0.97±0.02</td>
<td>0.77±0.09</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td>Chicks at 10 days</td>
<td>5.50±0.53</td>
<td>3.64±0.61</td>
<td>*</td>
</tr>
<tr>
<td>1983</td>
<td>Number of birds</td>
<td>13</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Clutch size</td>
<td>8.00±0.34</td>
<td>5.28±0.65</td>
<td>***</td>
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<tr>
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<td>Hatching success</td>
<td>0.75±0.11</td>
<td>0.38±0.13</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>Chicks at 10 days</td>
<td>3.23±0.68</td>
<td>0.45±0.21</td>
<td>***</td>
</tr>
<tr>
<td>1984</td>
<td>Clutch size</td>
<td>8.80±0.22</td>
<td>7.59±0.47</td>
<td>*</td>
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<tr>
<td></td>
<td>Hatching success</td>
<td>0.96±0.02</td>
<td>0.92±0.24</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td>Number of clutches</td>
<td>15</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chicks at 6 weeks</td>
<td>7.44±0.37</td>
<td>4.90±0.42</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>Number of broods</td>
<td>16</td>
<td>29</td>
<td></td>
</tr>
</tbody>
</table>

† Notes as in Table 1.

Table 3. Recapture of tagged chicks from hens treated with an anthelmintic and other hens from within the study area

<table>
<thead>
<tr>
<th>Year</th>
<th>Treated hens</th>
<th>Other hens</th>
<th>Significance*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1982 Tagged</td>
<td>44</td>
<td>159</td>
<td></td>
</tr>
<tr>
<td>Recaught (winter 1982, 1983)</td>
<td>12</td>
<td>30</td>
<td>$P &gt; 0.1$</td>
</tr>
<tr>
<td>1983 Tagged</td>
<td>37</td>
<td>115</td>
<td></td>
</tr>
<tr>
<td>Recaught (winter 1983)</td>
<td>4</td>
<td>9</td>
<td>Invalid†</td>
</tr>
<tr>
<td>Years combined Tagged</td>
<td>81</td>
<td>274</td>
<td></td>
</tr>
<tr>
<td>Recaught</td>
<td>16</td>
<td>39</td>
<td>$P &gt; 0.1$</td>
</tr>
</tbody>
</table>

* Levels of significance determined with 2 x 2 chi-squared.
† Numbers recaught after tagging were too small to allow a valid statistical comparison.

Fig. 1. The inverse correlation between breeding production (the ratio of young to old birds) and mean parasite burdens in old grouse within the main study area.
Comparison of breeding production and infection between areas

The inverse relationship (Fig. 2) between breeding success and the mean level of *T. tenuis* burdens in old grouse was significant in 4 out of 5 years (1979, $r = -0.90, P < 0.01$; 1980, $r = -0.63, P < 0.05$; 1981, $r = 0.20, P > 0.1$; 1982, $r = -0.76, P < 0.02$; 1983, $r = -0.72, P < 0.02$).
DISCUSSION

The treatment of hen red grouse with an anthelmintic reduced the burdens of T. tenuis and improved breeding production to 6 weeks of age. Since no difference was found in the subsequent recapture of immature birds reared by treated and untreated hens, respectively, the production of potential recruits within the study area was greater from hen grouse with lowered parasite burdens. Breeding production was negatively related to worm burdens, both within and between areas. Although these correlations do not themselves show cause and effect, the experimental findings illustrate that lowered worm burdens can improve breeding success; this improvement is consistent with the correlations (Fig. 3).

Fig. 3. A comparison of the experimental findings (data points) with regression lines from (a) Fig. 1, comparisons within an area; (b) Fig. 2, the common regression line for all years between areas; (c) the relationship used by Potts, Tapper & Hudson (1984) in their simulation model (---). The findings for treated (T) and untreated birds (UT) in each year of the experiment are represented by symbols (●).

An alternative explanation for the correlation between areas might have been that areas with poor food lead to low condition of hens which then get infected easily. Other workers have found food quality to be correlated with the breeding production of grouse (Moss, Watson & Parr 1975). More generally, it seems likely that the combined effects of malnutrition and parasite burden will influence body condition and together these affect breeding output, a relationship that has been demonstrated in a number of studies (Scrimshaw, Taylor & Gordon 1968; Rowland, Cole & Whitehead 1977; Solomons & Keusch 1981; Keymer, Crompton & Walters 1983).

Potts, Tapper & Hudson (1984) have produced a simulation model of a grouse population in which parasite burdens of breeding grouse are determined by the density of birds in the previous year. This level of infection then reduces the birds’ breeding production and so the number of birds subsequently shot. Sensitivity analysis of the model shows that this delayed density-dependent relationship between parasites on breeding success generates cyclic bag records in the model, similar to those observed on estates in the north of England. The relationship between breeding production and parasite levels used in the model is consistent with the experimental findings of this
study (Fig. 3), indicating that the measured effect of parasites on breeding production is large enough to account for the cyclic bag records observed. This model and experiment can explain the fluctuations in autumn density, and so the number subsequently shot, but may not account for fluctuations in breeding density.

Theoretical models (Anderson 1978; May & Anderson 1978) that incorporate a reduction in host fecundity through the effects of parasitism have also generated instability and, under certain conditions, cyclic changes in host numbers. Hudson, Dobson & Newborn (1985) applied one of these models to the grouse—T. tenuis system and generated cyclic fluctuations of a period similar to those observed in grouse populations. Together with the results of this study these findings provide evidence that parasites have a role to play in the population cycles of red grouse in England.

Long-term studies in Scotland have concentrated on the influence of intrinsic factors that cause fluctuations in breeding density. In a demographic study of a grouse population in north-east Scotland, Watson et al. (1984) developed a regression model incorporating the previous year’s sex ratio, the extent of summer emigration and the breeding success of grouse. The only observed extrinsic factor related to breeding production was the proportion of nests robbed by predators. This process alone could not account for the poor breeding observed and a better fit was obtained when intrinsic processes influencing emigration were incorporated. Although parasitism was not included in the model, the authors indicate that parasites, along with other extrinsic factors (weather, food and predation), may well affect productivity in other fluctuations. However, the effect of parasites on breeding production may have consequences for other aspects of the bird’s biology, such as spacing behaviour. Aggression between territorial neighbours will be expected to vary as a function of the coefficient of relationship between individuals, and this will vary with respect to breeding success and dispersal (Charnov & Finney 1980). Hence, the factors affecting breeding success could influence spacing behaviour, which in turn may influence winter dispersal. Our understanding of the role of intrinsic factors will be improved when the effects of parasitism can be specifically excluded.

When comparing these studies, it is important to note that the parasitism models of both Potts, Tapper & Hudson (1984) and Hudson, Dobson & Newborn (1985) were concerned with modelling the cyclic changes in bag records, whereas Watson et al. (1984) were modelling changes in breeding density. As such, the former will tend to emphasize the effects of breeding production and the latter the effects of over-winter survival and dispersal.

In summary, parasitic infection of red grouse on moors in northern England can reduce breeding production and modelling has successfully incorporated these effects as the main feature causing cyclic changes in numbers of grouse shot on these moors.

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REFERENCES


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