Preventing a population decline of red grouse *(Lagopus lagopus scoticus)* by manipulating density

A. Watson, R. Moss, R. Parr, I. B. Trenholm and A. Robertson

Institute of Terrestrial Ecology, Banchory, Kincardineshire, AB3 4BY (Scotland)
Received 21 September 1987; accepted 28 October 1987

Summary. This experiment tested whether a cyclic-type population decline can be prevented by removing territorial cock red grouse to keep breeding density below peak levels. The manipulated population did not decline, despite big decreases in food and breeding success, and more parasitic threadworms per bird than on the control.
Key words. Population cycles; red grouse; parasites; food supply.

Populations of lemmings, voles and hares[1], and grouse[2] often show population cycles (fluctuations in density more regular than would be expected by chance). Demographic models that explain cycles often involve the concept of delayed density-dependence, where losses to the population are related to its density one or more years previously[3]. No causal connection between densities and subsequent changes in numbers has yet been established, but popular suggestions include a reduction in food supplies[4] or an increase in parasitism[5, 6] or predation[7] following high densities. It is well established that all these factors can cause population declines, but it has not been shown that any of them act in a delayed density-dependent fashion to cause cycles. A more contentious idea is that intrinsic changes in the animals' own behaviour can cause cyclic changes in density, independently of the more obvious extrinsic limiting factors[8]. Theory, however, has outrun observation on cyclic populations, since not even the basic concept of delayed density-dependence has previously been tested experimentally. This paper describes an experiment designed to test the hypothesis[9] that, if a cyclic population is prevented from reaching peak density, it will continue to increase while a cyclic control population declines.

The work was done in north-east Scotland, a region where annual records of shot red grouse for more than a century show that numbers have exhibited cycles[10]. In our studies, including the present one, this cyclic pattern has continued in the absence of shooting. Previous experiments with red grouse in that region showed that fertilizing of their main food plant, heather (*Calluna vulgaris*), was sufficient to increase population density in some circumstances, but failed to prevent a big cyclic-type decline in numbers, which continued to extinction[11]. Demographic analysis and mathematical modelling of a cyclic-type population fluctuation lasting eight years from trough to trough indicated that the decline was caused largely by changes in spacing patterns, particularly by increases in emigration and territory size[12]. On the other hand, workers in north England found that hens given an anthelmintic drug reared more young[13], and claimed on the basis of modelling that changes in parasite burdens of the threadworm *Trichostrongylus tenuis* cause cyclic fluctuations in numbers of their red grouse hosts[6, 14]. A third set of workers have claimed (on the basis of correlation coefficients) that changes in breeding success cause fluctuations in spring numbers of *Lagopus* species, and that intrinsic factors (particularly changes in territorial behaviour) are unimportant[15]. The best clarification is a test by experiment.

Experimental procedure. The experiment was done on Rickarton moor near Aberdeen in east Scotland. The experimental area covered 203 ha of heather moor and the control 243 ha, excluding grass and wet bog seldom used by red grouse. Grouse numbers on the control were counted but not manipulated. A buffer area 0.4–1.0 km wide separated it from the experimental area. It was not possible to replicate the experiment fully because of the large study areas and intensive field work needed to do the experiment on the scale of an entire population. However, to increase the rigour of the experimental design, we published detailed predictions in advance[9]. Also, there were three separate years when numbers increased following annual manipulation on the experimental area while declining on the control areas, so each year can be regarded as a weak form of replication. Since a full replication would take eight more years covering another complete cycle, it seems reasonable to present the results now. This may encourage other workers to replicate our experiment, possibly on other species.

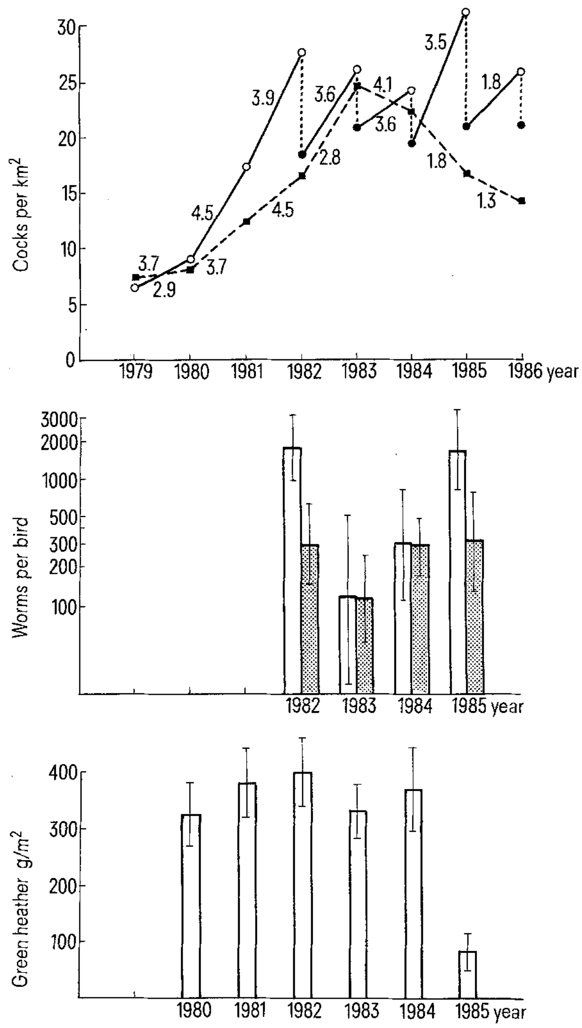
On the experimental area, the procedure was to keep breeding numbers down to approximately the 1981 level in each spring between 1982 and 1986. This was done by removing between 10 and 20 cocks each spring. There was no need to remove hens, as a similar number of hens which had been paired with these cocks then disappeared and presumably left the area, while the number of hens on the control area remained unchanged. Our counts showed all adult grouse present[12]; hence the main demographic data were on whole populations, not samples, and so not subject to sampling error. Nearly all territorial cocks were marked for recognition in the field, thus enabling us to achieve total individual enumeration of the cocks present. Observations of marked territorial adults showed very little movement between breeding populations on experimental and control areas.

The abundance of parasitic threadworms was assessed each spring by counting worm eggs in grouse droppings in March–April, and geometric mean worm numbers per bird were calculated (from a log/log regression of observed worm burdens on the number of worm eggs per g of caecal droppings from the same birds). Heather was sampled at the beginning of May, with green shoots separated by hand.

Results. On the control, numbers increased from a trough in 1979 and then conformed to our empirical demographic model of red grouse cycles[12], by peaking in 1983, and then declining (fig.) as predicted beforehand[9]. By 1986 there had been three years of decline on the control, but pre-removal spring numbers on the experimental area were higher each spring than they had been after removals in the previous spring. This result was obtained by removing cocks alone, thus indicating that in red grouse this sex controls breeding density.

Changes in spring numbers were not necessarily due to changes in breeding success. To the contrary, good breeding on the control area in the peak year, 1983, was followed by a decline in spring density. Although the big decline in spring density on the control from 1984 to 1985 was associated with poor breeding there in 1984, very poor breeding on the experimental area in 1985 was followed by an increase in spring numbers. Hence poor breeding may precede some declines but does not necessarily cause declines. The generally poor breeding in 1985 followed severe desiccation and browning[16] of heather shoots in late winter 1985, which reduced the amount of green heather per unit area by about 80%. Despite this, grouse density on the experimental area again increased in spring 1986, although it continued to decline on the control.

Threadworm burdens were generally below the level of 3000–4000 worms per bird where a reduction in host condition would be expected from work by others[17]. Even so,



Spring density and breeding success of red grouse on experiment and control, numbers of parasitic threadworms *Trichostrongylus tenuis*, and amount of green heather. Top: Number of cocks per km² in spring on experimental area (○ —— ○ ······ ●, vertical dotted lines showing experimental reductions) and control (■– – – – –■), and number of young per hen in August on experiment (upper of each pair of values) and control (lower of each pair). Middle: worm numbers on experiment (open) and control (stippled), with 95% confidence limits (bars). Bottom: dry weight of green heather shoots per m² in spring, with 95% confidence limits (bars). Data are for both areas combined; results on experiment and control differed little, and both showed a big decline of green shoots in 1985.

when burdens differed between our areas, they were higher on the experimental area. Despite this, it was the control population that continued to decline and the experimental population to increase, as we had predicted. This prediction was based on our empirical demographic model[12], which did not specify the biological mechanism involved in causing population cycles. Our view, on the basis of past studies, is that the mechanism is change in the birds' own spacing behaviour[9] (territorial behaviour, aggression and emigration), but the present experiment did not test this explicitly. Work to test predictions from this hypothesis is now in progress. Decreases in food supply or breeding success, and increases in parasite burdens, can sometimes be correlated with declines in spring grouse densities, and may be useful in mathematical models for predicting future grouse stocks. Our experiment shows, however, that they are not necessary for population declines to occur. High density on the control was followed by a decline down to a level well below that on the experimental area. In contrast, the experimental population was prevented from reaching breeding densities high enough to precipitate a decline as on the control. To conclude, delayed density-dependent declines can occur independently of food, parasite burdens, and breeding success, and if peak densities are not reached a decline need not occur.

This experiment on grouse had similarities with previous cropping experiments on small rodents[18]. These failed to put experimental populations out of phase with their controls, but all had problems in design or execution. It would now seem worthwhile attempting rodent experiments again.

Acknowledgment. We thank Dr B. Staines for comments.

1 Begon, M., Harper, J. L., and Townsend, C. R., Ecology. Individuals, Populations and Communities. Blackwell, Oxford 1986.
2 Watson, A., and Moss, R., Ornis fenn. *56* (1979) 87.
3 Varley, G. C., and Gradwell, G. R., A. Rev. Ent. *15* (1970) 1.
4 Keith, L. B., Oikos *40* (1983) 385.
5 Anderson, R. M., and May, R. M., J. Anim. Ecol. *47* (1978) 219.
6 Potts, G. R., Tapper, S. C., and Hudson, P. J., J. Anim. Ecol. *53* (1984) 21.
7 Pearson, O. P., J. Anim. Ecol. *35* (1966) 217.
8 Chitty, D., Proc. ecol. Soc. Aust. *2* (1967) 51.
9 Moss, R., and Watson, A., Symp. Br. ecol. Soc. *25* (1985) 275.
10 Williams, J., Oecologia, Berl. *65* (1985) 269.
11 Watson, A., Moss, R., and Parr, R., J. Anim. Ecol. *53* (1984) 663.
12 Watson, A., Moss, R., Rothery, P., and Parr, R., J. Anim. Ecol. *53* (1984) 639.
13 Hudson, P. J., J. Anim. Ecol. *55* (1986) 85.
14 Hudson, P. J., Dobson, A. P., and Newborn, D., in: Ecology and Genetics of Host-Parasite Interactions, p. 77. Academic Press, London 1985.
15 Bergerud, A. T., Mossop, D. H., and Myrberget, S., Can. J. Zool. *63* (1985) 2240.
16 Watson, A., Miller, G. R., and Green, F. H. W., Trans. bot. Soc. Edinb. *40* (1966) 195.
17 Hudson, P., Red Grouse. Game Conservancy Trust, Fordingbridge 1986.
18 Krebs, C. J., Keller, B. L., and Tamarin, R. H., Ecology *50* (1969) 587.

0014-4754/88/030274-02$1.50 + 0.20/0