Population Cycles and Parasitism

Hudson et al. (1) used anthelmintics to reduce worm burdens in cyclic red grouse (Lagopus lagopus scoticus) managed for shooting, and claimed to have stopped population cycles. Their study may be an important demonstration that wildlife diseases can have a strong impact on host dynamics (2), but the statement that “these results show that parasites were both sufficient and necessary in causing cycles in these populations” (1) seems unwarranted, for two reasons.

First, Hudson et al. based their interpretation on large reductions in the amplitude of the 1989 and 1993 declines in grouse numbers in response to treatment, but their measure of grouse numbers was the number of birds shot, not the population size. Indices of population size such as sequential hunting or trapping statistics invariably overestimate the variance in population size when compared to direct counts (3). Hudson et al. compared numbers of grouse shot with numbers actually counted in one control area and showed that variance in the former was at least tenfold larger than in the latter. No attempt was made to shoot birds in 1989 and 1993 in five out of six untreated control populations (4). If the increased variance caused by the sampling process (shooting) is taken into account, it can be inferred that at least 100 birds per square kilometer were present on the control areas in 1989 and 1993. Further, gamekeepers knew the treatment allocations because they were the people treating grouse with anthelmintics, and this could have significantly biased the shooting effort. Thus, there are insufficient data to accurately estimate differences in cycle amplitude between control and treated areas.

Second, despite Hudson et al.’s claim that cycles were stopped, cyclic fluctuations took place on treated areas where parasitism was reduced. Cycle amplitude varies greatly in red grouse populations (as in other species) with cyclic dynamics (5). Parasite dynamics is thought to be dominated by rainfall—which affects the survival of free-living parasite larvae (6)—in drier parts of Scotland, where low amplitude cycles with periods of up to 10 years take place and where parasites are thought not to cause cycles (6, 7). Thus, observing a reduction in cycle amplitude in response to anthelmintics while retaining cyclic dynamics is entirely consistent with hypotheses relating cyclic dynamics to processes other than parasitism (7). Hudson et al. have provided evidence for reduced fluctuations as a consequence of anthelmintic treatment, but the evidence for a change in fluctuation pattern is equivocal.

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References and Notes
4. Numbers in (1), figures 1A and 2, A and C, are actually number shot + 1 as data were plotted on a logarithmic scale. This was not specified in the report.
8. 24 April 1999; 20 August 1999

Response: Lambin et al. state that we should have used sample counts, not bag records, for our analysis. Their main concern is that the variance in bag records is large at low grouse densities. However, our data show that a decrease in variance only occurred when grouse densities were relatively high, greater than 110 birds per square kilometer (1). Underlying this result is a strong relation between bag records and sample counts that is only slightly confounded by the variance in bag records.

References and Notes
1. P. J. Hudson et al., Science 282, 2256 (1999); P. J. Hudson, Grouse in Space and Time (Game Conservancy Trust, Fordingbridge, U.K., 1992), figure 4.2, Levene’s test for homogeneity, F = 1.91, P = 0.045. Decrease in variance with mean sample count r = 0.69, P < 0.05.

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