

Mountain hares, louping-ill, red grouse and harvesting: complex interactions but few data

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Introduction

Our recent paper examined the impact of a large-scale field manipulation of mountain hare density on the dynamics of ticks, louping-ill and red grouse (Laurenson *et al.* 2003). We found that hares were an important host for ticks and for the transmission of louping-ill, and that tick burdens and louping-ill seroprevalence in grouse declined when hare densities were reduced, in comparison to a control. In addition, the number of young grouse produced per adult bird increased, but no effect on grouse density was found. Our model of the system showed that the dynamical decline in louping-ill can be accounted for through the decline of both ticks and the process of non-viraemic transmission. Cope, Iason & Gordon (2004) make two broad sets of observations on this study. First, they comment on the limitations of the controls. Secondly, they make minor modifications to an existing model of nematode-driven grouse cycles, replicating previously published research (Hudson *et al.* 2002) and use it to confirm the same finding that louping-ill virus may be expected to dampen grouse cycles. Combined, the authors use these observations to argue that a policy of reducing mountain hare density to keep grouse moors economically viable has not been proven and go on to imply that louping-ill may even improve the economics of grouse harvesting.

In reply, we argue that while we agree that the controls presented in our paper were not ideal, they remain informative. In this respect, our hypothesis that hares are a reservoir host for louping-ill remains the most plausible explanation for the observations made over our 9-year study. Cope *et al.* neither propose an alternative hypothesis to explain our observations or present data to refute this hypothesis. They also fail to understand the difference between a vector and a host: mountain hares are not a vector of this virus. Secondly, our group has already shown that there is good theoretical evidence that louping-ill dampens population cycles and some empirical evidence supports the theory (Hudson

et al. 2002). Indeed, the bifurcation figures in that work show more clearly than Cope *et al.*'s repetition that grouse density and harvests might be reduced by louping-ill. However, as we did not have sufficient data in our recent study with which to test this hypothesis we touched only briefly on this issue in our discussion. Thirdly, while these simple models lead Cope *et al.* to suggest that increased red grouse mortality from louping-ill improves harvesting returns and thus also grouse moor economics, we argue that their treatment of this question is poorly founded, as it fails to consider the full suite of complex issues (such as thresholds for harvesting or maximizing long-term income) affecting the economics of grouse harvesting.

Study design

Many of the concerns expressed by Cope *et al.* over the controls are addressed by a careful reading of our paper. For example, we did not use the site adjacent to Control 1 site, where tick control on sheep was poorer than at other sites, to either explain absolute differences in tick abundance or examine the effect of mountain hare removal on tick abundance, as Cope *et al.* suggest. In contrast, it was used to examine the relative importance of different species as tick hosts. As a further example, Cope *et al.* suggest that changes in hare culling at Control 1 site in 1999 mean that the significant reductions we found in tick numbers and louping-ill prevalence are invalid. We disagree: as stated in our original paper, there appears to be a 2-year time lag for management changes to have an effect on both these factors, due most probably to the length of the tick life cycle. Moreover, reanalysis of these data over the period 1993–99 shows that the relationship between the decline in tick numbers and louping-ill prevalence over the shorter period is also highly significant (interaction between site and year: larvae, $F_{5,839} =$, $P < 0.001$; nymphs, $F_{5,839} = 11.5$, $P < 0.001$; LI prevalence, $\chi^2 = 13.5$, d.f. = 1, $P < 0.001$).

Control site 2 was chosen to examine the effect of a decline in louping-ill virus on grouse breeding success and density for the very reason that it would take account of the underlying cycles in grouse abundance, although Cope *et al.* claim that we ignored this issue.

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Time-series analysis of harvesting records (Haydon *et al.* 2002) reveals the same pattern of fluctuations occurring in the same phase at the treatment and control site as is evident from Fig. 2b in our original paper. Although we agree that perfect controls would be sites with comparative levels of louping-ill virus, this does not invalidate our analysis as the louping-ill prevalence at the treatment site declined to that at the control site. We do not attempt to explain absolute differences in grouse breeding success or density between treatment and control sites – rather, we compare relative temporal changes, when other potential factors (apart from a decline in louping-ill virus) are held at their original levels. Thus, as long as other factors which might be important in determining grouse breeding success, such as game keeper density, soil quality and heather productivity are held constant, and the effects of climate are comparatively similar at both sites (which should be the case as they are geographically close), using this control site to examine relative temporal changes would take account of cyclic changes.

In summary, while we agree that a large-scale, fully replicated and ideally controlled field experiment is the best way to examine this issue, we fear that study sites for such work are most probably unavailable in Scotland. As we discussed at some length in our paper, the difficulties of this approach are again exposed with the conflicting demands of scale, replication and correct controls (May 1999). In this respect, many ecologists now appreciate these limitations and consider that time-series analysis coupled with the results from manipulations such as ours provide an informative insight into identifying the most parsimonious hypothesis for underlying processes (e.g. Hilborn & Mangel 1997; Ellner 1989; Turchin 2003). If the understanding of large-scale population processes can be based only on fully replicated and controlled field experiments, our knowledge of the underpinning tenets of their ecology and epidemiology would be extremely curtailed.

The impact of louping-ill on red grouse and its implications for management

Cope *et al.* highlight an apparent paradox in our study in finding a significant increase in relative breeding success after louping-ill declined, but no significant change in relative red grouse density. This is not uncommon in experiments on birds (Newton 1998) and could be explained quite simply by either a lack of power or an increase in harvesting intensity in response to the increased productivity. Indeed, harvests have increased nearly 40-fold at the treatment site over the period of the study, with no downturn to date (unpublished data). As we state in our paper, more time-series data would clarify these issues.

Cope *et al.*'s minor modification of a previous model confirms that, theoretically, louping-ill may shorten and dampen grouse cycles (Hudson & Dobson 2001; Hudson *et al.* 2002). They then reiterate the hypothesis

that a reduction in louping-ill virus would increase the maximum and decrease the minimum points of grouse cycles (Hudson 1992; Hudson & Dobson 2001). This hypothesis is not new and is supported by previously published data (Hudson 1992; Hudson & Dobson 2001). Cope *et al.* also assert, for reasons that are not made clear, that the median population size over the period of the cycle is an appropriate metric of potential harvest value but fail to consider both high infection rates, such as were observed in our study (> 95%), and the implications of the unsymmetrical changes in cycles generated by their model. The key point for grouse moor managers trying to maximize revenue is that an indication of maximum revenue is best described by the total area under the curve and not by the metric that might best describe the midpoint of the cycle.

Extending the conclusions from these models to discussion of the impact of louping-ill on grouse-moor economics is clearly difficult ground. The relationships between patterns of variability, harvesting returns and economic returns are particularly complex and have been the subject of a great deal of attention from resource modelers and managers. Cope *et al.*'s superficial and entirely data-free discussion of this issue in relation to grouse harvesting and their suggestion that louping-ill may improve economic returns is far from convincing and fails to include any new insights. They ignore key features particularly relevant in this system: the nature of the relationships between densities, harvest levels and economic returns.

Non-linearities and even threshold effects occur when managers consider the level of and type of grouse harvest to take (Cattadori *et al.* 2003). Models suggest that driven shooting is viable only when densities over 60 birds/km² occur (Hudson 1992), although this is variable and most managers would choose a higher threshold. Below this threshold most managers do not shoot at all, in order to allow for overwinter mortality. Some limited harvesting may be conducted by walking up or shooting over pointer dogs. The importance of this issue is well illustrated by drawing potential thresholds on Fig. 1 in Cope *et al.* and examining in which scenarios low or no harvests may be taken. The distinction between driven shooting and other types is also critical when considering revenues. Driven grouse command a fee approximately double that per bird compared to other types of harvesting, although annual overheads for moorland management are more or less constant. Thus financial returns are unlikely to be related linearly to harvest level.

With such potential complexity and non-linearities, Cope *et al.*'s suggestion that louping-ill (and thus any type of generalist predator) improves the economic returns from moorland is fragile at best. Further analysis of harvesting records are clearly required to examine how maximum financial returns and harvests can be achieved in cyclic grouse populations, where economic returns may not be related linearly to harvest levels. We look forward to seeing such an analysis.

In conclusion, although we neither carried out nor claimed to have carried out a fully replicated and controlled large-scale field experiment we believe the available evidence remains supportive of the hypothesis that mountain hares are an important host for the louping-ill virus and its vector. Although the controls were not ideal their use was misrepresented by Cope *et al.*, who offer no alternative explanation for our findings. Their slightly modified model does not extend insights gained from previously published work. An entirely different set of analyses are required from the ones presented to examine the complex relationship between louping-ill prevalence, grouse densities and harvests and the economics of harvesting. Until that is carried out, an extended discussion of this topic is likely to remain academic.

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