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Harvesting unstable populations: red grouse *Lagopus lagopus scoticus* (Lath.) in the United Kingdom

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The optimal harvesting strategies for unstable populations are explored using first discrete time models and second a continuous time model specifically applied to the destabilising effects of the caecal nematode *Trichostrongylus tenuis* on the dynamics of red grouse *Lagopus lagopus scoticus*. In discrete time models, with overcompensation generating either cyclic or chaotic fluctuations in abundance harvesting can act as both a stabilising and a destabilising process. Maximum yields occur at the harvesting rate that coincides with the point where the harvesting stabilises the overcompensation. Optimal harvesting rates increase with the degree of overcompensation although these are more vulnerable to over-harvesting. Harvesting in the continuous time model provides similar results, although observed hunting records do not appear to be stabilised by harvesting. Empirical data on the mortality caused by other natural enemies of red grouse, the hen harrier *Circus cyaneus* and the louping ill virus, show that these mortalities do stabilise grouse dynamics. One explanation is that both hen harriers and louping ill virus cause significant mortality to chicks before the infective stages of *T. tenuis* are laid down on the ground, whereas shooting takes place after the infective stages are laid down and thus do not stabilise the populations.

Key words: harvesting, parasites, population cycles, population dynamics, red grouse

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Harvesting strategies of natural resources do not have a healthy history (Milner-Gulland & Mace 1998). Several species have either been driven to extinction or are now listed as threatened, often as a consequence of greed and ignorance. Yet, with increased demand for sustainable use of natural resources there is still a pressing need to identify harvesting strategies that will provide a sustainable and optimal yield. In the case of game species, the decisions on harvesting strategy are left to either the hunter or the biologist. The traditional, long-term strategy of an unregulated hunter is to use trial and error in a manner that allows a reasonable and sustainable harvest to be identified. Hunters often attempt to harvest the potential recruitment with the objective of leaving a constant breeding population. A strategy that

may work in practice but not necessarily an approach that will provide the optimal yield and potentially one that would lead to overexploitation. The strategy of the biologist is to harvest the population to the level where the density-dependent compensation produces the maximum numerical harvest. While this is a theoretically fine strategy, it is of course naive, and in many instances, particularly in marine fisheries, the case of the simple Maximum Sustainable Yield (MSY) approach has often ultimately proved disastrous (Hilborn 1996, Hilborn & Mangel 1997, Ludwig, Hilborn & Walters 1993). Invariably this is because workers have failed to comprehend either the mechanism or the nature of the density dependence. Furthermore, most harvested species have high rates of fecundity and, consequently, pop-

ulations are not stable; the density-dependent response by the population is rarely immediate and there are frequently spatial and temporal heterogeneities that can lead to potentially disastrous errors in the estimate of optimal harvesting strategies. The hunter appears to be practically right but optimally wrong, whereas the biologist is theoretically correct and practically wrong. Is it reasonable to suppose that the problems that have been observed are a consequence of not understanding the nature of the underlying density dependence?

Many harvested gamebirds exhibit unstable population dynamics. For example, most species of grouse together with a number of species from the Phasianidae exhibit cyclic fluctuations in abundance (Hudson 1992, Tapper 1992, Lindström, Ranta, Kaitala & Lindén 1995, Cattadori & Hudson 1999). Workers generally agree that the likely cause of these oscillations is overcompensation in the density-dependent mechanism although we must acknowledge that there are still debates about the precise nature of the mechanisms involved. In this paper, we address the specific question: how should unstable populations be harvested? The elegant approach would be to develop a simple analytical model and identify a clean answer, but unfortunately this is not so simple. Nevertheless, since we have an insight into the various mechanisms that may cause cycles, we can use specific models and simulations to identify general rules of harvesting. We explore these questions by starting with a simple extension of the Maynard Smith & Slatkin (1973) model for density-dependent recruitment. We then examine the unstable population dynamics of red grouse *Lagopus lagopus scoticus* as a worked example. Red grouse are eminently suitable since our own work has provided good evidence to suppose that the main destabilising process is the parasite-induced reduction in the breeding production (Hudson 1986, 1992, Dobson & Hudson 1992, Hudson, Newborn & Dobson 1992, Hudson, Dobson & Newborn 1998).

Harvesting an unstable population: overcompensation in discrete time models

Simple, discrete time models can be used to generate a wide range of dynamics from monotonic damping through damped and stable oscillations to chaos (May & Oster 1976, Hassell, Lawton & May 1976). We apply the discrete time model presented by Maynard Smith & Slatkin (1973) in which changes in abundance, N , are determined by the density-dependent net reproductive rate, $F/(1 + aN_t)$, and the degree of compensation, b :

$$N_{t+1} = (s - h)N_t \left(1 + \frac{F}{(1 + (aN_t)^b)}\right)$$

When b is less than unity, undercompensation occurs and the simulations exhibit monotonic damping. When b is equal to one, there is perfect compensation, but with values larger than unity overcompensation occurs, and with sufficiently large values of the reproductive rate, F , cycles and chaos can be recorded (Hassell et al. 1976). We incorporated harvesting by reducing survival, s , by the harvesting rate, h ($(s - h)N_t$), and then selected values of b and the reproductive rate, which would produce three clear types of dynamics: monotonic damping, cycles or chaos. Then using variations in harvesting pressure plotted stock-recruitment curves and harvest-yield relationships (Fig. 1).

When $b = 1$ and the model produced simple monotonic damping, the outputs (see Fig. 1A) were similar to those recorded in text books and show a simple hump-backed relationship with the maximum sustainable yield (MSY) coinciding with the point where recruitment is maximised (e.g. Milner-Gulland & Mace 1998). When there is overcompensation and the dynamics become cyclic, the situation is somewhat different; the harvesting first amplifies, then dampens the oscillations and the maximum yield occurs just before the point where the harvesting pressure effectively stabilises the overcompensation and the population stops oscillating. However, this maximum yield is now at a greater harvesting rate than the monotonic case and vulnerable to overharvesting. Harvesting of the chaotic dynamics may appear complex (see Fig. 1C), but the general sustainable solution is similar. The MSY again coincides with the point where the harvesting effectively eliminates the overcompensation, but the yield here is higher than the previous two cases and more vulnerable to overharvesting. Note, however, that when the harvest rate is reduced, the average yield may remain the same but be more variable, and this is likely to be the optimal and safe solution.

In general terms, the MSY occurs at the harvesting rate that effectively just eliminates the overcompensation in the population and stabilises the population (Fig. 2). This situation is more vulnerable to overharvesting.

Case study: harvesting strategy of red grouse

In this section we examine in detail a specific system and use continuous time models to determine if the findings of the previous section are borne out when the density-dependent mechanism is known. First, we describe the unstable dynamics of red grouse and the harvest-

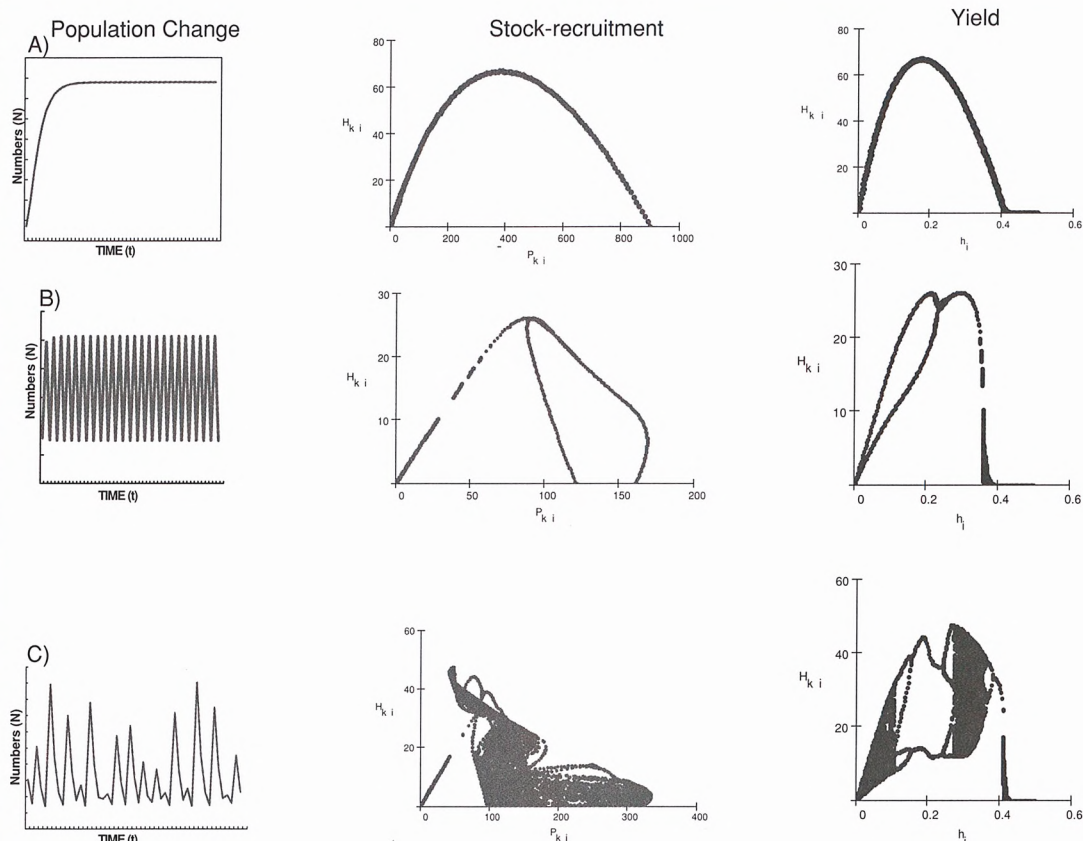


Figure 1. Population changes, stock recruitment and harvest yield curves produced from a harvested Maynard Smith & Slatkin (1973) model with variations in overcompensation of the density dependence that generate A) monotonic damping ($b = 1$); B) cyclic fluctuations ($b = 5$); C) chaos ($b = 10$) (other parameters: $s = 0.5$, $F = 6$, $a = 0.01$).

ing strategy used to harvest the population. Second, we describe the destabilising process and then seek the optimal harvesting strategy. Third, we examine the consequence of other natural enemies on the harvesting of the system and compare observed dynamics with the simulations from the model.

Harvesting records

Analyses of hunting records have shown that red grouse populations in both England and Scotland exhibit cyclic fluctuations in abundance (Hudson 1992). These reflect the underlying variations in grouse abundance although Lambin, Krebs, Moss, Stenseth & Yoccoz (1999) pointed out that bag records may overestimate the variance in population size because hunters would tend not to harvest at low densities. A preliminary examination of the data confirms that variance does increase when grouse count densities are below 100 birds

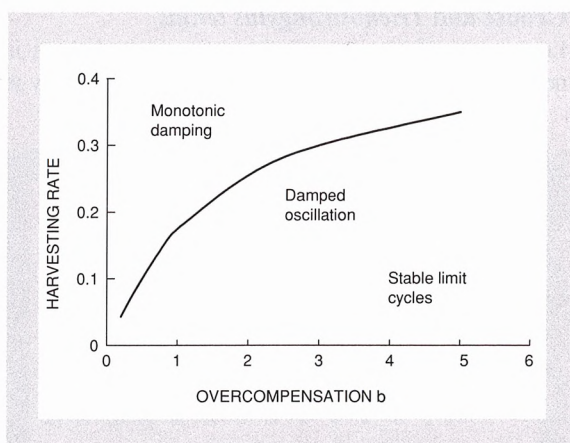


Figure 2. Maximum yield curve derived from the Maynard Smith & Slatkin (1973) model. The harvest rate that produced the maximum yield increased with the degree of overcompensation in the density dependence and occurred at the point where the instability is removed from the population.

km⁻² (Hudson, Dobson & Newborn 1999). However, a more detailed analysis of the count data shows that variance in the counts falls with the mean of the counts ($r = -0.69$, $P < 0.05$) such that at low densities there was more variation between count areas than recorded at high densities. In this respect the variance is really in the counts because when grouse numbers fall the grouse population is aggregated in areas and are not distributed evenly throughout the habitat. As such, bag records provide a better reflection of what is happening at the population scale than the more precise counts conducted at a smaller scale.

Harvesting strategy

The majority of red grouse in the United Kingdom are harvested during driven grouse shooting, where the birds are pushed from an area of suitable habitat over a line of hunters. We attended 22 grouse-shooting days and found that each hunting day typically consisted of 8.4 hunters or guns (range: 6–12) and 16 beaters (range: 15–19). The guns stand in stone or wooden built hides known as butts, and the beaters 'drive' grouse from an area of approximately 150 ha. Typically four drives are undertaken during each hunting day. The grouse fly over the guns in groups that can consist of more than 100 individuals. Proportionately fewer grouse were shot from the large groups than from the small groups (Fig. 3), and since the singletons tended to be old males, these may be considered selectively harvested from the population (Hudson 1985).

Continuous time models for red grouse

Grouse and *Trichostrongylus tenuis*

Long-term monitoring of red grouse populations in northern England has shown that cyclic declines in

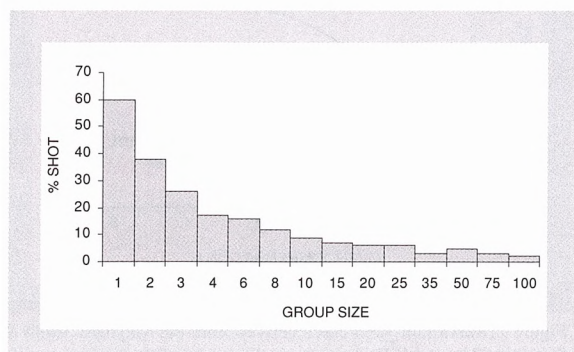


Figure 3. Harvesting of red grouse in relation to group size as recorded on 22 hunting days. Hunters selectively shot grouse as singletons, many of which were old males (Hudson 1985).

grouse numbers are associated with an increase in the intensity of infection with the caecal nematode *Trichostrongylus tenuis* (Hudson et al. 1992). Population growth rate falls and breeding mortality increases with the intensity of the infection in the population (Hudson et al. 1992, 1998). Experimental field studies, in which parasite intensities are reduced, have shown that parasites are the cause of reduced breeding production and the major cyclic declines in abundance observed (Hudson 1986, Hudson et al. 1992, 1998).

The findings from these experimental studies together with other laboratory studies on the life cycle of the parasite have been incorporated in a three-equation analytical model based on the original Anderson & May (1978) macroparasite-host model (Dobson & Hudson 1992). The model describes changes in host, adult parasite and the free-living stages of the parasite (further details and parameter estimates are available in Dobson & Hudson (1992)). Cyclic fluctuations in abundance occur when the degree of parasite aggregation in the host population is low and is less than the ratio of the parasite-induced reduction in host mortality to the reduction in fecundity. In essence, this means that with the low level of aggregation observed in this system, the parasite-induced reduction in fecundity will destabilise the system and cause oscillations of the period, amplitude and pattern observed in the bag records (Potts, Tapper & Hudson 1984, Dobson & Hudson 1992). The findings concur well with both the field observations and experiments although there are other hypotheses for the cause of cycles in red grouse.

Harvesting the grouse model

To investigate the optimal yield from the system, a constant harvesting rate was applied to the population

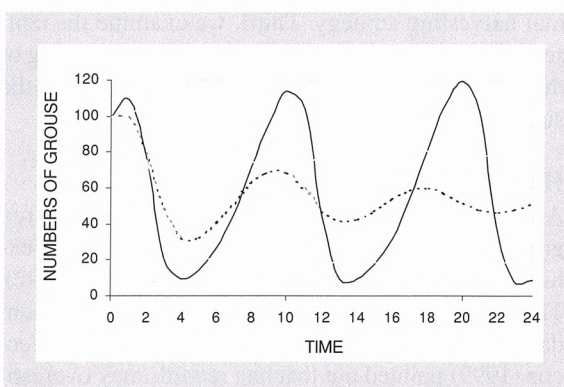


Figure 4. Simulations from the continuous time model in relation to increasing harvesting rate. Increasing harvest rate initially dampened the oscillations but increased overall population size (large dashes and then dots) while high harvesting rates led to a reduction in population size (small dashes).

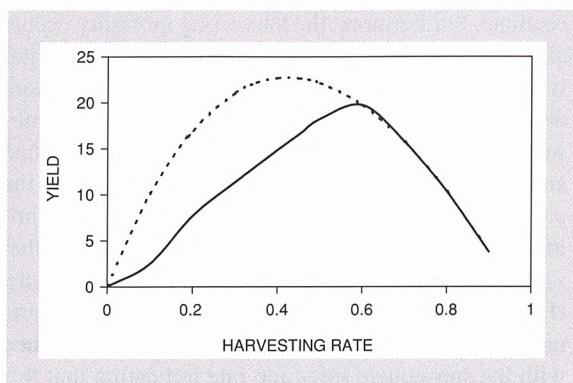


Figure 5. Harvest yield curves for the grouse/*T. tenuis* continuous time model without (—) and with the impact of parasites (---). Note that incorporating parasites increased the harvesting rate that generated the maximum yield.

of grouse in the model and yield-harvest curves generated. The effect of harvesting was to reduce the size of the population, reduce infection rate and thus stabilise the population's tendency to oscillate (Fig. 4). Harvest yields increased to the point where the population stopped oscillating (Fig. 5). When the model was run without the parasite induced effects, then the yield curve produced a typical hump-backed yield curve with a higher yield but at a lower harvesting rate.

As the hunters selectively shot the adult male grouse that flew over the guns as singletons, and as these have larger worm burdens than the immature grouse (Hudson 1986), this would have a larger impact on the worm population than the grouse population. The consequence of this would be to reduce the effects of parasite induced mortality and this again would lead to an increase in the grouse population, and consequently higher yields

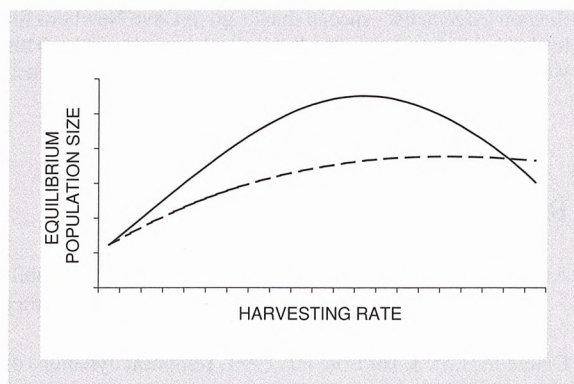


Figure 6. Influence of harvesting (—) and selective harvesting (---) on the equilibrium population size of grouse determined from the continuous time model. Both harvesting strategies increase the size of the grouse population, but the selective harvesting removes a higher proportion of the heavily infected grouse leading to a larger increase in population size (see Hudson, Dobson & Newborn 1992 for more details).

(Fig. 6). In other words, selective harvesting increases the equilibrium population size, a counterintuitive and interesting observation.

In summary, this exploration of the specific grouse/*T. tenuis* model provides a similar conclusion to that observed in the discrete time model: optimal yields arise at the point where the instability is removed through harvesting.

Grouse and natural enemies

The analyses of the models indicate that harvesting should be a stabilising process that dampens population oscillations. Clearly the harvesting of grouse has not dampened oscillations since the majority are highly unstable (Hudson & Dobson 1996). As such we must address the question why do harvested populations continue to oscillate when the models indicate they should be dampened? We shall examine this question in the Discussion, but before doing so it may be instructive to examine the consequence of other mortalities on the population dynamics of red grouse, viz. those induced by natural enemies. We shall consider first predation by hen harriers *Circus cyaneus*, and second pathogen induced mortality by the tick-borne louping ill virus.

Predation by hen harriers

A recent intensive study on the effects of raptor predation on red grouse numbers found that following the establishment of hen harriers on one grouse population, the predation caused by the harriers dampened the cyclic fluctuations in abundance (Thirgood, Haydon, Rothery, Redpath, Newton & Hudson 2000). Numbers of red grouse (counts and harvest) fell so that an expected cyclic fluctuation, as predicted using an ARMA model, failed to occur. In contrast, two neighbouring populations where harriers had not established showed the predicted cyclic fluctuation. The main impact of the harrier predation on the red grouse population is to catch young grouse chicks and hens just before incubation (Redpath & Thirgood 1997). This leads us to suppose that the predation caused by the harriers effectively stopped a cyclic fluctuation in red grouse numbers because the hen harriers were significantly reducing the breeding production of the grouse.

Parasitism and louping ill virus

Louping ill is a viral disease transmitted by the sheep tick *Ixodes ricinus*, which causes 80% mortality in red grouse exposed to the virus (Hudson 1992, Hudson, Norman, Laurenson, Newborn, Gaunt, Reid, Gould, Bowers & Dobson 1995). The ticks that transmit the virus are

active during the main spring months, and thus coincide with the hatching of the grouse so that much of the mortality occurs in the young grouse. Grouse populations with louping ill virus consistently have lower breeding densities, higher breeding mortality and lower bag records (Hudson 1992). Time series analyses of hunting records show that populations with louping ill virus have significantly lower partial autocorrelation functions at a time lag of two years than populations without louping ill virus (P.J. Hudson, unpubl. data). In other words, populations with louping ill virus exhibit a reduced tendency to oscillate compared with populations without louping ill virus. As with the predation study by Thirgood et al. (2000), much of this mortality occurs on the young grouse and the effect appears to be to stop the population from oscillating.

Discussion

Both the discrete time and continuous time models lead us to the conclusion that maximum yields from unstable populations occur when the harvesting pressure effectively eliminates the cause of the instability. This is generally true for both cyclic and chaotic dynamics although the optima for the overcompensating density dependence is at a higher harvesting rate than the direct density dependence and so the populations are vulnerable to overharvesting. Indeed, at lower harvesting rates a more variable harvest will occur but this may provide, on average, an acceptable and safer long-term harvesting strategy.

Both types of model identify that yields will be greatest when the dampening effects of harvesting stop the population from oscillating. In the specific worked example of red grouse, the data from the monitoring and field studies show that the natural predators (hen harrier and louping ill virus) did indeed dampen the oscillations in the population, but the human induced harvesting did not have any significant influence. One explanation is that harvesting is causing such low mortality as to have little impact on the population dynamics. This is unlikely to be the case as field data have shown that hunting mortality can be significant, in some areas as high as 50% of the population (Hudson 1985, 1986). An alternative explanation is that the natural enemies are reducing the density of the population before the infective stages of the parasitic nematode *T. tenuis* are laid down on the ground thus reducing the subsequent density-dependent infection rate. In turn these low levels of infection will reduce the impact of the parasite and the tendency of the population to

oscillate. Furthermore, the harvesting mortality occurs after the birds have already contaminated the habitat with parasite infective stages. Thus bird and parasite density prior to harvesting have determined the subsequent infection rate for birds that are not harvested and the population continues to be influenced by the parasite. This is supported by observations on the timing of infection in grouse, as observations show that young grouse are infected during July and early August (Hudson & Dobson 1996) while the harvesting starts on 12 August. Moreover, density in July is correlated with the subsequent infection rate indicating that this is the density of grouse that lays down the infective stages (Hudson et al. 1992).

The important lesson to learn from this investigation is that a misunderstanding of the mechanism of density dependence can lead to an erroneous harvesting strategy. Not only do the mechanisms need to be identified, but also the timing of events must be considered. While parasites appear to have a major impact on red grouse populations in our study areas and at these times, this is not to say that some other density-dependent mechanism may not be influencing other populations at other times. In conclusion, optimal harvesting strategies for unstable populations should increase effort until the tendency of the population to oscillate begins to decline, assuming that the optimal yield occurs at the point where the populations cease to cycle. However, extreme care should be taken; first, because these optima are frequently close to the levels of exploitation where the population collapses, and second, a detailed understanding of the nature of the density dependence is needed to examine when the timing relates to harvesting.

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