

PASTURES, PESTS AND PRODUCTIVITY: SIMPLE GRAZING MODELS WITH TWO HERBIVORES

Summary: Simple grazing models with two herbivores are used to assess the effects of pasture pests on stability and productivity of continuously-growing pastures. Algebraic and graphical methods are also presented for estimating losses from pasture pests at different stocking rates directly, from data on productivity/stocking rate relationships.

Pests are considered as competing grazing herbivores and denuders of pasture area. Denuding pests have no effect on stability but grazing pests increase the likelihood of discontinuous stability. The forms of the damage function and its dependence on stocking rate are described for both types of pest.

Estimating losses from pasture pests by an equivalent reduction in stocking rate can give useful 'best bet' results even when the true effect is to reduce per capita productivity at fixed stocking rates. However, the first will overestimate or underestimate the second in particular situations, depending on the level of the fixed stocking rate relative to the economic optimum.

Actual economic losses for rabbits and porina caterpillars, representing grazing and denuding pests, are estimated as \$2.1/rabbit and \$0.08/porina m²/stock unit carried, based on a reduction in stocking rate. At a fixed optimum stocking rate losses are 300% greater, and at a fixed 75% optimum stocking rate losses are 60% less.

Given the sensitivity of losses to stocking rate, field trials to estimate pest or weed effects should assess their impact on stocking rate rather than their effect on productivity at a fixed stocking rate whose relationship to the theoretical optimum is unknown.

The equilibrium model is shown to apply to seasonal pastures, but regular variations in growth rate reduce productivity and increase stability, converting some discontinuously stable systems into continuously stable ones. The likelihood of discontinuous stability appears in any case remote.

The 'laissez-faire' herbivore/vegetation model (the 'extensive' equivalent of the one described in this paper, with herbivore numbers varying) can not be applied to more than one herbivore.

Keywords: Pasture pests; pest management; pest model; grazing model; sheep grazing; Wiseana; Hepialidae; stocking rate; pasture production

Introduction

Noy-Meir (1975, 1976, 1978a, 1978b) demonstrated how simple, 2-equation predator/prey models could provide useful insights into the dynamic behaviour of managed grazing systems, their stability and the relationship between total stock intake or productivity and stocking rate at equilibrium. That is, parameters are assumed to remain constant so that a balance is eventually achieved between growth and consumption and the vegetation reaches a steady state. This paper briefly reviews the essential features of Noy-Meir's models, then considers their validity in the more realistic situation of seasonally varying vegetation growth rates.

The models are then extended to a situation with two herbivores grazing a single resource, in order to deduce the effects of pasture pests on the stability of a grazing system, the general forms of the damage functions, and some estimates of economic losses. Grazing models with two herbivores have not

previously been considered, and the predator/prey equivalent has also received little attention (but see May *et al.*, 1979).

The treatment of a pest's competitive effect is expanded to include not only grazing but also removal of plant cover. This is a qualitatively different effect, since the pest removes resource 'capital' as opposed to 'interest'. Many invertebrates effectively feed in this way (Harris and Brock, 1972; Davidson, 1979; Barlow, 1985a), and are referred to here as 'denuding' as opposed to 'grazing' pests. Weeds such as thistles and rushes have the same effect - removal of pasture area - for a different reason.

Finally, brief consideration is given to 'extensive' two-herbivore grazing models, in which herbivore numbers vary.

Models

The simple equilibrium model

Noy-Meir's models reduce a grazing system to its

dynamic essentials, namely the equilibrium states achieved through the interaction between growth and consumption, both expressed as functions of the amount of vegetation present. These functions can take a number of different forms, and the results of 16 combinations have been analysed for vegetation/single herbivore systems by Noy-Meir (1978b). Rather than consider all of these, the present paper uses growth and consumption functions which recent evidence suggests are among the most realistic and at the same time embody all the qualitative features likely to be revealed by alternative models.

A typical growth function for the vegetation is:

$$G = \frac{rV(1-V/K)}{1 + \frac{(1-2p)V}{p^2 K}} \tag{1}$$

where G = net growth rate (kg green dry matter (DM) ha⁻¹ day⁻¹)

r = maximum specific growth rate (G/V as V → 0)

V = vegetation density (kg green DM ha⁻¹)

K = vegetation density at which growth is zero (kg green DM ha⁻¹)

p = V at which G is maximised, as a proportion of K (i.e. G is a maximum when V = pK).

Maximum net growth rate G_x = rp²K (= rK/4 for the symmetrical, logistic growth curve).

This is a general function giving a dome-shaped curve which is symmetrical, peaked to the right or peaked to the left, depending on the value of p. Rightward-peaked vegetation growth curves (p > 0.5) have not been observed, however.

Provided p < 0.5, equation 1 can be partitioned into an asymptotic, Michaelis gross growth function and a linear senescence one, with senescence rate m (= rp²/(1-2p)):

$$G = \frac{(r+m)V}{1 + \frac{rV}{mK}} - mV$$

If p = 0.5 (the logistic), equation 1 partitions into a logistic rather than Michaelis gross growth curve and a linear senescence function.

The growth function is also equivalent to function G3 in Noy-Meir (1978b) and when plotted is virtually indistinguishable from the gross growth curve of White *et al.* (1983) combined with linear senescence:

$$G = (r+m) V \frac{(1+r)^{-V/K}}{m} - mV$$

The consumption function for herbivore 1 (the stock) is assumed to take a sigmoid form:

$$C_1 = \frac{H_1 c V^2}{a^2 + V^2} \tag{2}$$

where C₁ = consumption rate for H₁ individuals of herbivore 1 (kg green DM ha⁻¹ day⁻¹)

c = maximum per capita consumption rate

a = vegetation level at which consumption is 50% of the maximum

This function embodies limitation by appetite at high vegetation levels, and by ability to prehend herbage and maintain bite size at low vegetation levels. However, the growth and consumption functions could equally relate to the multiplication of scattered items or clumps of palatable food, and their discovery and ingestion by searching herbivores; such a situation is more analogous to predation.

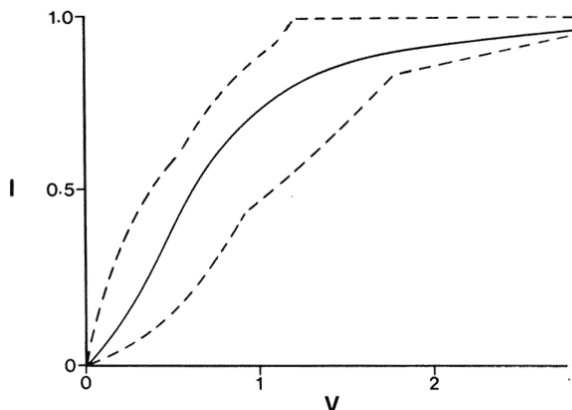


Figure 1: Relative intake (I) in relation to green herbage Present (V, tones green DM ha⁻¹). — Model, - - - - - Outer bounds of a range of published relationships (Bircham, 1981; Arnold and Dudzinski, 1967; Freer *et al.* 1970; McKinney, 1972; Vickery and Hedges, 1972; Arnold, Campbell and Galbraith, 1977; Curll and Davidson, 1977; White *et al.*, 1983).

Fig. 1 shows that a per capita consumption function (i.e. C₁/H₁) with a = 600 is a reasonable compromise among a range of published curves for sheep. The overall grazing model is thus:

$$V = \frac{rV(1-V/K) - \frac{cH_1 V^2}{a^2 + V^2}}{1 + \frac{(1-2p)V}{p^2 K}} \tag{3}$$

= 0 at equilibrium

Finally, a generalised function for animal productivity relates this linearly to intake:

$$p = gH_1 \left[\frac{cV^2}{a^2 + V^2} - f \right]$$

Where g = a conversion factor
 f = maintenance requirement or per capita intake rate at which productivity is zero, in terms of DM ingested
 P = productivity (e.g. weight gain $ha^{-1} Day^{-1}$, milk yield $ha^{-1} day^{-1}$)

To exemplify the grazing situation the parameters are initially given the following values, characteristic of a New Zealand pasture set-stocked with hoggets: $K=4000$, $Gx=30$, $c=2$, $a=600$, $g=0.187$, $f=0.8$. P (productivity) in this case measures liveweight gain. In practice, two values for the growth curve parameter (p) are of interest. $p = 0.5$ gives a symmetrical logistic or sigmoid growth curve, which is well-known and widely used (Brougham, 1956; Christian *et al.*, 1976; Noy-Meir, 1976). $p = 0.35$ gives an asymmetric, leftward-peaked curve which recent evidence suggests is more realistic, at least for continuously grazed swards (Bircham and Hodgson, 1983; Parsons *et al.*, 1983). Since the two growth functions are standardised to the same Gx and K , r is different for each (0.03 for the logistic, 0.061 for the asymmetric).

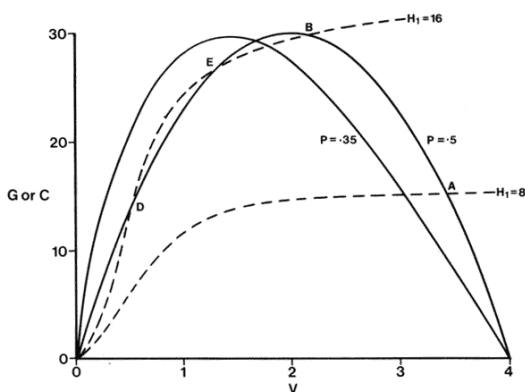


Figure 2: The relationship between rates of growth (G , —) or consumption (C , - - -), both $kg\ ha^{-1}\ day^{-1}$ and green herbage present (V , tonnes green DM ha^{-1}). The two growth curves correspond to different values of p , and the two intake curves to different stocking rates, H_1 . Points A, B, D and E are described in the text.

Fig. 2 shows consumption rates for two stocking rates and both growth curves (logistic and asymmetric) as functions of V . Such a grazing system is well described by Noy-Meir (1975) and May (1977) but will be briefly reviewed here. In Fig. 2 the vegetation will stabilise where the curves intersect and growth equals consumption (e.g. point A). The vegetation level and stocking rate at which this occurs are denoted \bar{V} and \bar{H}_1 . If some disturbance causes V to exceed \bar{V} , then consumption exceeds growth and V therefore declines back to \bar{V} ; if V drops below \bar{V} the reverse occurs and V increases back to \bar{V} . The equilibrium point at A is therefore stable, meaning that the vegetation will return to its original state following disturbance. Points B and D are similar but point E is different, since an increase in V causes growth to exceed consumption and V to increase still further. E is therefore an unstable equilibrium point.

For the logistic growth curve, at low stocking rates a single, stable equilibrium exists at A in Fig. 2. As stocking rate increases (i.e. the total consumption curve rises), \bar{V} declines and the single equilibrium is suddenly replaced by three, two of which are stable (B and D) and one unstable (E). At such a stocking rate (16 in Fig. 2), if V is below E the system will tend to point D; if above E then it will tend to the upper equilibrium at B. Such a system with multiple stable equilibria is referred to as discontinuously stable (Noy-Meir, 1975).

Figs. 3a and b show the isoclines representing \bar{V} values for every \bar{H}_1 , given by the intersections in Fig. 2 for different stocking rates but calculated in practice from equation 4. The isocline for the logistic model (Fig. 3a, solid line) exhibits a discontinuity or fold, and hence a safe capacity (Noy-Meir, 1978b) or maximum stocking rate at which a single, stable equilibrium exists. For other growth/consumption curves there may also exist a 'maximum capacity', the stocking rate at which $\bar{V} = 0$. In Fig. 3b no such stocking rate exists, and maximum capacity will be set by the minimum per capita intake necessary for survival rather than exhaustion of vegetation. Figs. 3c and d (solid lines) show the productivity/stocking rate relationships at equilibrium for the two models (i.e. the values of P corresponding to the \bar{H}_1 and \bar{V} combinations, from equation 3). Productivity per unit area increases then declines with increasing stocking rate, the decline being considerably less steep for the asymmetric growth model than for the logistic. In fact the curve for the former is not unlike the empirical model of Jones and Sandland (1974) and may provide some theoretical basis for their observed relationship.

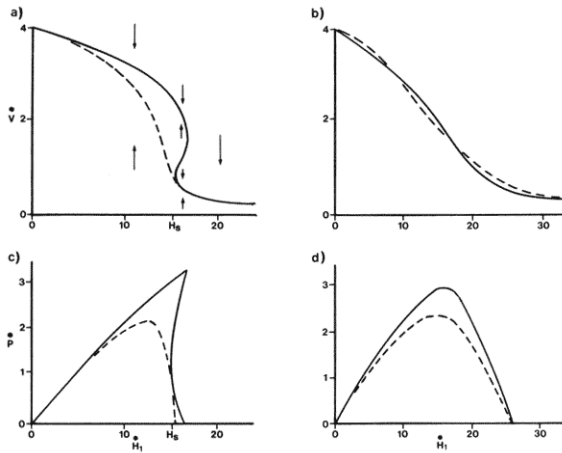


Figure 3: a) and b) Relationships between equilibrium Vegetation levels (\bar{V} , tones green DM ha^{-1}) and stocking Rate (H_1 , sheep ha^{-1}) for the logistic (a) and asymmetric (b) growth models. — constant growth, - - - - - seasonally varying growth. Arrows denote direction of change of the vegetation and H_s the safe capacity (see text). c) and d) Relationships between productivity at equilibrium (P , kg weight gain $ha^{-1} day^{-1}$) and stocking rate (H_1) for the logistic (c) and asymmetric (d) growth models. The dashed line in d) represents both seasonally varying growth and constant growth with $r=0.07$ and $K=3000$.

The significance of discontinuous stability lies in the fact that small incremental increases in stocking rate can give sudden and dramatic reductions in herbage levels and productivity (Figs. 3a and 3c), and that to re-establish the original state, stocking rate may have to be reduced well below the point at which the decline in vegetation originally occurred. In other words, there is a hysteresis effect in which an undesirable state is more readily achieved than cured; the greater the fold in Fig. 3a the greater the problem of recovery. This fold may also be referred to as a simple catastrophe, in fact the simplest possible (Saunders, 1980). Productivity is maximised in Fig. 3c at the stocking rate at which the discontinuity occurs, so in a variable environment the gains from maximising stocking rate must be balanced by the increased risk of collapse. As Noy-Meir (1975) points out, discontinuous stability also implies that experimental trials involving continuous uncontrolled variation in initial herbage levels may yield two qualitatively different outcomes in terms of productivity under the same (high) stocking rate (see

Fig. 3a). By contrast, the system involving the asymmetric growth curve in Fig. 2 is continuously stable; there exists only one stable equilibrium at all stocking rates up to the maximum sustainable. This is fairly obvious by inspection of the shapes of the curves in Fig. 2, and can be demonstrated numerically by solving equation 3 for H , in terms of V , given the parameter values and in particular the value of p determining the shape of the growth curve. Unfortunately the system has no simple analytical solution, hence no explicit criteria for discontinuity except when $p = 0.5$ (the logistic). In this case it is discontinuously stable if $a/K < 1/3\sqrt{3}$. (May 1977). More generally, as Noy-Meir (1978b) points out, discontinuous stability is most likely in systems where a is small (i.e. consumption satiates at low V) relative to pK (the level of V at which growth peaks).

Model with varying growth rates

In most temperate pastures, growth rates vary seasonally and the equilibrium model, which assumes that r and K are constant and the vegetation stabilises at some fixed level, is no longer strictly applicable. However, while the vegetation level will change in a seasonal model, there is clearly a steady state possible at any given stocking rate, such that total herbage gains balance total losses over the year. The question therefore arises as to whether the conclusions of a simple equilibrium model change when it is applied to a pasture in long-term equilibrium but with a seasonally varying growth rate. In particular, is the stability of the system and the relationship between average vegetation level and stocking rate affected, and does the productivity/stocking rate curve change?

Noy-Meir (1978a) addressed the problem of seasonality in terms of changes in V over a fixed period corresponding to the growing season. The approach adopted here was to run the model as a simple simulation with K and G_x varying sinusoidally throughout the year with amplitudes of $\pm 50\%$ and 75% respectively.

The outcome is shown by the dashed lines of Fig. 3. The effect is to increase stability, converting the discontinuously stable model into a continuously stable one (Fig. 3a), and to displace the productivity/stocking rate curves downwards and to the left (Fig. 3c). Maximum productivity is thus reduced, and the decline in productivity at high stocking rates is also less marked. The productivity/stocking rate curve for the variable asymmetric growth model (Fig. 3d) is virtually identical to one for an equilibrium model with reduced

K (3000) and G_x (26 instead of 30) (Fig. 3d), but in the second case the stable vegetation levels corresponding to each H_i are considerably lower than the average levels under variable growth.

It seems likely, therefore, that conclusions from simple equilibrium models will apply to seasonal pastures with the qualifications that the effective values of K and G_x (but not necessarily r) are lower than their actual means, stability is greater and the decline in productivity at high stocking rates less marked. Numerical studies suggest that the increased stability manifested in Fig. 3a only occurs if the period associated with the variation is long. Discrete, regular yearly or half-yearly variations in growth parameters have a similar effect to the sinusoidal oscillation, but shorter periods of alternating or randomly varying values, as a result of weather effects on pasture growth for example, have much less effect on the shape of the solid curve.

The effects of pests are therefore considered in relation to the asymmetric equilibrium growth model with adjusted parameter values $K = 3000$ and $G_x = 26$ ($r = .07$), giving the dome-shaped productivity/stocking rate curve in Fig. 3d (dashed line). Experimental evidence and the results of more detailed models also suggest that this shape is realistic (Jones and Sandland, 1974; White *et al.*, 1983; Monteith, 1972; Suckling, 1975), but the consequences are briefly considered of a more steeply descending curve such as that in Fig. 3c (dashed line). Numerical studies confirmed that the effect of pests predicted by the seasonally varying model was the same as that predicted by the modified equilibrium one.

Results

Effects of grazing pests

If the consumption function for the second herbivore (pest) takes the same form as that for the stock (H_1), the overall model is:

$$V = \frac{rV(1 - V/K) - \frac{cH_1V^2}{1 + \frac{(1-p)V}{p^2k}} - \frac{dH_2V^2}{a^2 + V^2}}{b^2 + V^2}$$

where d = maximum consumption rate of the pest (kg green DM $ha^{-1} day^{-1}$)

$b = V$ at which individual consumption rate is half maximum

H_2 = pest density (ha⁻¹)

In this case the equivalent isocline diagram to Fig. 3b will have a second horizontal axis representing the

equilibrium pest density, \hat{H}_2 at right angles to that for \hat{H}_1 , and the \hat{V} versus \hat{H}_1 and \hat{H}_2 relationships will form a surface. If there is a fold in either the \hat{V}/\hat{H}_1 or \hat{V}/\hat{H}_2 relationships, then the overall system will be discontinuously stable and there will be a range of \hat{H}_1 and \hat{H}_2 , combinations for which two stable vegetation equilibria exist (Fig. 4). The 3-dimensional fold in Fig. 4 is known as a cusp catastrophe (Saunders, 1280), after the shape of its projection onto the \hat{H}_1/\hat{H}_2 axis and as distinct from the 2-dimensional fold catastrophe of Fig. 3a. Thus, if one of the two herbivore/vegetation systems is discontinuously stable, so too will be the combined system. The presence of pests will therefore convert a continuously stable grazing system into a discontinuously stable one if b is small. Though little data exist, this may well be the case, since pests are generally smaller than the productive stock and presumably more efficient at grazing low levels of vegetation. Two extreme situations can thus be envisaged, in which consumption is unaffected by vegetation availability ($b = 0$) or is affected in the same way as for the stock ($b = a$).

Figs. 5a and b show the effects of grazing pests such as rabbits at $60 ha^{-1}$, with potential daily intake $d = 0.2$ and $b = a = 600$ or $b = 0$. With $b = 600$ there is no effect on stability, since the pest is equivalent to additional stock units (1 pest = d/c stock units), and the shape of the vegetation isocline in Fig. 5a remains the same. The effect on productivity is to displace the curve in Fig. 5b downwards and to the left. This is characteristic of all negative influences on the grazing system, such as reductions in pasture exponential growth rate r or ceiling yield K , and variability in growth (Fig. 3d). The two important consequences are that the absolute reduction in productivity is greater at a high initial stocking rate (e.g. the optimum of $15 ha^{-1}$ in Fig. 5b) than at a lower one, and that at a high initial stocking rate, productivity in the presence of the pest is maximised by reducing the stocking rate. As a corollary, this shows why many farmers stock at a lower level than might be suggested by average pasture growth rates; variability in growth reduces the optimum stocking rate (Fig. 3d). Further, the effect of successive displacements of the productivity curve due to increasing pest densities is to reduce productivity at any fixed stocking rate by ever greater amounts, since the stocking rate now corresponds to the declining portions of the new curves. The effect of the pest on productivity is thus non-linear, and the steeper the right hand side of the productivity/stocking rate curve the greater the non-linearity and the effect of the pest.

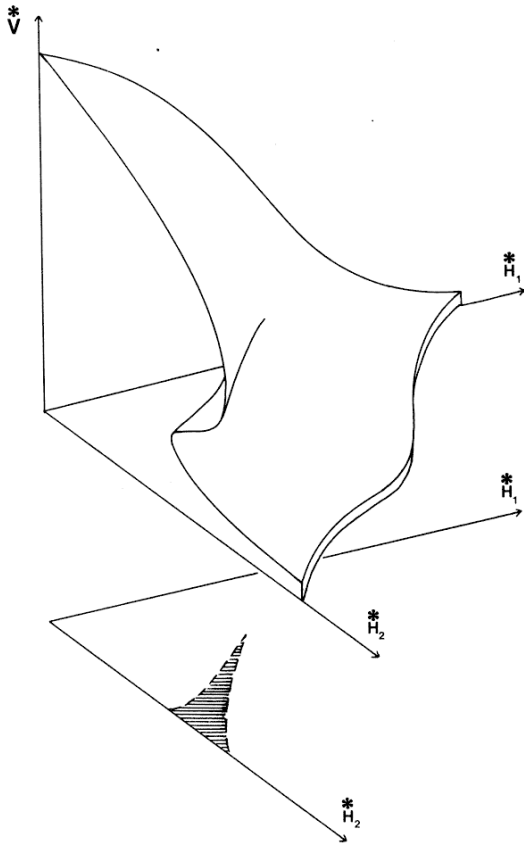


Figure 4: The surface giving equilibrium vegetation levels (\bar{V}) as functions of stock (\bar{H}_1) and pest (\bar{H}_2) densities, where the individual stock/vegetation system is continuously stable and the pest/vegetation one is discontinuously stable. The shaded area represents a projection of the fold in the surface onto the \bar{H}_1/\bar{H}_2 plane, and the combinations of \bar{H}_1 and \bar{H}_2 at which two stable and one unstable vegetation equilibria exist.

The equilibrium logistic model in Fig. 3c represents the extreme case, in which the system would become suddenly unstable for a small additional increment in pest density.

If the ultimately efficient grazing pest is now considered, for which $b = 0$, the vegetation isocline takes a different form (Fig. 5a). The system is discontinuously stable and has a maximum sustainable stocking rate in the presence of the pest (10.6 in this example). Moreover, there is a lower critical level of \bar{V}

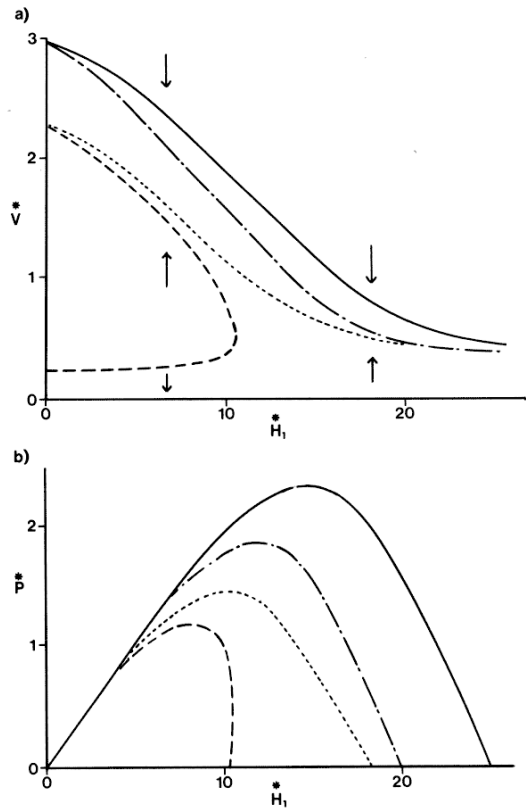


Figure 5: a) The effects of grazing pests such as rabbits, and denuding pests such as porina larvae (*Wiseana* spp.) on the equilibrium vegetation (\bar{V} , tonnes green DM ha^{-1})/stocking rate (\bar{H}_1) relationship for the modified asymmetric growth model (see text). — no pests, - - - - grazing pests at 60 ha^{-1} , $b = a$; - - - - grazing pests at 60 ha^{-1} , $b = 0$; - - - - denuding pests removing 20% pasture area. Arrows indicate direction of vegetation change. b) The effects of pests as above on the equilibrium productivity (\bar{P} , $kg\ ha^{-1}\ day^{-1}$)/stocking rate (\bar{H}_1 , sheep ha^{-1}) relationship.

(about 200 kg/ha^{-1} in Fig. 5a) such that if \bar{V} once falls below this, no reduction in stocking rate will permit recovery. The effect on productivity is also more dramatic, with the pest's impact and the steepness of the right hand side of the productivity/stocking rate curve both greatly increased (Fig. 5b); the latter also implies greater non-linearity in the pest density/productivity relationship.

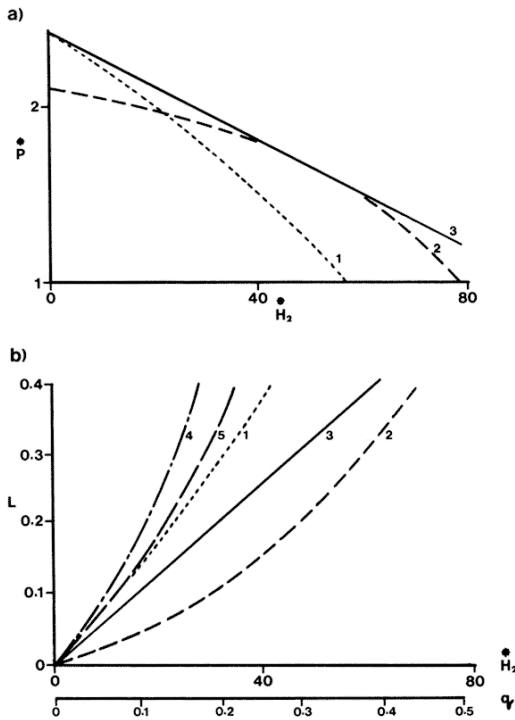


Figure 6: a) The effect of grazing pests (\bar{H}_2 , rabbits ha^{-1}) on equilibrium productivity (\bar{P} , kg weight gain $ha^{-1}day^{-1}$) at different stocking rates: 1(-----) fixed, optimum (15 sheep ha^{-1}); 2(——) fixed, 75% optimum (11.25 ha^{-1}); 3 (——) variable, optimum at all pest densities. b) The damage function for grazing and denuding pests: proportional losses in productivity (L) in relation to grazing pest density (\bar{H}_2 , ha^{-1}) or proportional loss in pasture cover (q). Curves 1, 2, 3 as above, for grazing pests with $b=a$ at different stocking rates; 4 (-----) grazing pest with $b=0$, stocking rate optimum; 5 (——) denuding pest, stocking rate optimum. Curve 3 (——) also represents the effect of a denuding pest on stocking rate if per capita productivity is maintained irrespective of the initial stocking rate.

The shapes of the relationships between productivity and pest density are shown explicitly in Fig. 6a for initially optimum and 75% optimum stocking rates (15 and 11.25 ha^{-1}) and for stocking rate which is varied so as to maximise productivity at any pest density, in all cases for $b = a$.

Varying the stocking rate gives a linear relationship, and losses arise from the stocking rate reduction equivalent to the pest density (based on the ratio of potential consumption rates of each if $b = a$, that is, 60 pests ha^{-1} equate to 6 stock units ha^{-1} if $d = c/10$). In Fig. 6b, losses are expressed as proportions, so the slope of the line would be different at different initial stocking rates. For instance, if stocking rate were adjusted to be always 75% of the optimum rather than the optimum, per capita productivity would be higher and the effect of a given pest density would therefore be the same loss in stock units but a greater loss in total productivity. Moreover, the initial per hectare productivity would be lower. For both reasons, therefore, the proportional loss and the slope of the solid line in Fig. 6b would increase at sub-optimum stocking rates. This applies only to grazing pests (see below).

At a fixed stocking rate, per hectare losses are due to a reduction in per animal productivity and tend to be non-linearly related to pest density (Fig. 6a), as discussed above.

Fig. 6b shows the damage functions, relating losses to pest density for high, low and varied stocking rates. In the first two cases initial losses, whether expressed as percentages or in absolute terms, are respectively greater and less than those if stocking rate is varied. Fig. 6b also shows the more non-linear function for $b = 0$ at the fixed optimum stocking rate.

Particularly for invertebrate grazers, the pest's effect may be concentrated in patches. If the stock are assumed to be mobile over the whole area, V in a pest-infested patch will be the same as that over the rest of the area. Per capita consumption rate of the pest will therefore be the same within the patch as it would be outside it, and since the pest's contribution to overall consumption depends only on the per capita consumption rate and on the product of (density x proportion of area infested), the effect of patchily-distributed grazing pests is equivalent to that of uniformly distributed ones at a corresponding lower density. In fact, unless the damage functions in Fig. 5 are linear it is essential to average pest densities over the whole farm before calculating per hectare losses. The estimate of losses based on the average whole-farm pest density (or cover loss in the case below) is then divided by the proportion of the farm affected to give per hectare losses on that portion (Barlow, 1985a).
Effects of denuding pests

The situation is now considered in which a certain proportion of the pasture is totally denuded of

palatable vegetation by the action of a pest, weed or anything else. In other words, what is the effect of the loss of a given area (effectively an increase in stocking rate) rather than the loss of a given daily increment through grazing? The crucial difference is that the loss in potential growth through grazing depends only on the consumption rate of the pest, whereas that lost through denuded cover depends both on the area affected and the potential growth rate of the pasture. In other words, the effects of a denuding pest on pasture and animal productivity would be expected to be proportional rather than absolute; a given area denuded would give greater losses in a high-producing, highly-stocked pasture than in a low-producing one. A steady state is assumed, which can represent any of the following situations: (a) the proportion bare actually increasing owing to continued pest attack, but assumed to be constant at its mean level over the period considered; (b) the aftermath of pest attack, with no compensation by the vegetation; (c) recolonisation by vegetation balancing its continued removal by pests, the proportion bare reaching a steady value.

The effects of denuded pasture on equilibrium vegetation/overall stocking rate relationships are more easily derived than are those of a grazing pest. Productivity per unit total area is given by equation 4 as before, where H_1 is again the number of stock per unit total area. However, the equilibrium vegetation level is lower since the effective stocking rate on the vegetated area is now $H_1/(1-q)$ where q is the proportion of pasture lost. Per capita consumption rate $cV^2/(a^2 + V^2)$ in equation 4, hence P , is therefore reduced. As for a grazing pest with $b = a$, there is no effect on the system's stability (Fig. 5a) and the productivity/stocking rate curve is displaced downwards and leftwards with no significant change in shape (Fig. 5b). Again, therefore, losses are considerably greater at a high stocking rate than at a low one and increase non-linearly with pest density (Fig. 6b); small reductions in pasture area, particularly at low stocking rates, have little effect on productivity but this effect rapidly increases as additional pasture is lost. As Fig. 5b suggests, reducing stocking rate maximises productivity and, other things being equal, the proportional reduction will equate to the proportional pasture loss whatever the initial stocking rate. The slope of the solid line in Fig. 6b is thus constant, whereas that for a grazing pest increases at sub-optimum stocking rates (see above). Lost pasture area is assumed directly proportional to pest (or weed) density (e.g. McLaren and Crump, 1969; Barlow,

1985a), though in the case of weeds there will be some variation due to differences in individual plant sizes, and in the case of pests there may be competition at high densities, reducing the denuded area per pest. The latter will tend to reduce the non-linearity in the productivity/pest density relationship.

Economics of Pasture Pest Attack

The economic effect of pests is most easily assessed in terms of a stocking rate reduction. For grazing pests, dollar losses per hectare (D) are simply:

$$D = GM \cdot H_2 d / c$$

that is, the gross margin per stock unit (GM) multiplied by the pest's equivalent in stock units (i.e. the product of pest density and the ratio of consumption rates, if $b = a$). Taking $GM = \$21$ for a sheep breeding system (Anon, 1986) and $d/c = 0.1$ gives losses for rabbits of $\$2.1/\text{rabbit}$.

For a denuding pest, losses equate to the per hectare gross margin ($GM \cdot H_1$) multiplied by the proportional loss in pasture area, q :

$$D = GM \cdot H_1 H_2 q'$$

where q' = average area removed per pest so that $q = q' H_2$. Thus, the moth larva *porina* (*Wiseana* sp.) denudes an average of 36 cm^2 of pasture area over a year (Barlow, 1985a), and using $GM = 21$ gives losses of $\$0.076/\text{stock unit}/\text{porina m}^2$. Losses from a denuding pest therefore depend on gross margin per hectare, whereas those from a grazing pest depend on gross margin per stock unit.

Economic losses are much more difficult to assess if stocking rate is maintained in the face of pest attack, but the simple grazing model, and in particular Fig 6b, allow some useful approximations to be made. It is necessary, first, to assume that the dome-shaped productivity/stocking rate curve of Fig. 5b, upon which Fig. 6b is based, is realistic as a general description. This seems a reasonable assumption in terms of its derivation and agreement with empirical data (see below). If so, then changing the parameters f and g of equation 4 to include variable costs per stock unit and price per unit product will change the axes of Fig. 5b but not its shape (see Appendix I). The shape of the resulting gross margin $\text{ha}^{-1}/\text{stocking rate}$ curve also agrees with the results of experiments and more detailed models (e.g. White *et al.*, 1983; Spath, Morley and White, 1984). Thus, the proportional reductions in productivity given by Fig 6b can also be interpreted as proportional reductions in per hectare gross margin.

Although the curves 1 and 2 in Fig. 6b are non linear, for moderate pest infestations (about 10% in terms of lost pasture area or the pest's equivalent in stock units relative to the actual stocking rate), their initial slopes compared with that of line 3 give an indication of the losses due to pests at fixed stocking rates, relative to those if stocking rate is reduced. The curves are similar for denuding and grazing pests (compare curves 1 and 5 in Fig. 6b). Such a comparison suggests that the formulae for losses given above must be multiplied by a factor of approximately 1.2 if stocking rate is held constant at the economic optimum, and 0.5 if it is constant at 75% of the optimum. The latter is an average figure and in practice differs slightly for grazing and denuding pests. Thus, losses at a fixed stocking rate may be greater or less than those if it is reduced, depending on the level of the fixed stocking rate relative to the economic optimum. If the latter is unknown, therefore, it seems reasonable to approximate losses at a fixed stocking rate by those calculated more easily on the basis of a stocking rate reduction.

Applying the above factors to rabbits and porina gives the estimates of losses in Table 1. Allowing for differences in costs and prices, the results for porina are similar to those from the more detailed model of Barlow (1985a).

Table 1: *Estimates of economic losses caused by rabbits and porina caterpillar in a sheep breeding enterprise. These assume a gross margin per stock unit of \$21 (1986 prices) and change proportionally as this value changes, either for other stock classes or with changes in costs and prices. SU=stock unit.*

	Economic Losses	
	\$ per rabbit	\$/SU/porina m ²
Stocking rate reduced; per animal output maintained	2.1	0.076
Stocking rate constant at the economic optimum	2.5	0.091
Stocking rate constant at 75 % optimum	1.1	0.038

All these results relate strictly to sustained pest attacks. For short-term ones it is necessary to assume that the response is rapid and that the effect, over the period for which it acts, is equivalent to that of the same sustained change. The other assumption, that losses at fixed stocking rates are linearly related to pest density when the latter is low, can be relaxed and explicit values given for any pest density and stocking rate, if the productivity and per hectare gross margin versus stocking rate curves (e.g. Fig. 5b) are

approximated by an equation of the form:

$$P = uH - vH^\theta \dots\dots\dots 5$$

This describes dome-shaped curves with varying degrees of asymmetry. For instance, Jones and Sandland (1974) show that many experimental trials yield a productivity per hectare/stocking rate relationship which is a combined linear/quadratic equation, similar to equation 5 with $\theta = 2$. Stocking rate trials of Monteith (1972) and Suckling (1975) yield per hectare gross margin/stocking rate curves for sheep systems of the same form with $\theta = 3$ and $\theta = 2$ respectively, given meat and wool outputs and 1986/87 costs and prices (Anon, 1986). The detailed model of White *et al.* (1983, Fig. 8) gives a net income per hectare/stocking rate curve fitted by equation 5 with $\theta = 3$, and the model of Spath *et al.* (1984, Fig. 2b) yields one with $\theta = 2.5$. The adjusted asymmetric model above (Fig. 3d, dashed line) is similar to equation 5 with $\theta = 3$ but has a slightly sharper peak. Given this equation, therefore, if effective stocking rate increases by a factor s ($= 1/(1 - \text{proportion denuded})$) for a denuding pest, and $(1 + dH_2/cH_1)$ for a grazing pest), then the factor by which productivity or gross margin change is:

$$F = \frac{\theta - (sh)}{\theta - sh} \theta^{-1}$$

where h = stocking rate/optimum stocking rate (see Appendix 2). Given data like the above, which enable the actual productivity or gross margin/stocking rate curve to be estimated, this formula allows losses to be estimated independently of the grazing model.

Even more directly, losses can be estimated graphically from a curve fitted statistically or by eye to the data (e.g. the solid line in Fig. 7). The productivity/stocking rate curve (dashed line in Fig. 7) for any percentage cover loss from a denuding pest, or grazing pest density (with $b = a$), is most easily constructed by considering the stocking rate reduction needed to maintain per capita productivity. For a denuding pest this must equal the percentage pasture loss and for a grazing pest it is the pest's equivalent in absolute stock units (dH_2/c). Given an arbitrary initial stocking rate D , and its per hectare productivity ED , B is the point on OE (i.e. with the same per capita productivity) such that BF ($=cD$) equals the stocking rate reduction, either as a percentage of OD or as the required fixed number of stock units. Repeating the process for a set of initial stocking rates, D , gives the corresponding points, B , hence the dashed curve for that pasture loss or pest density.

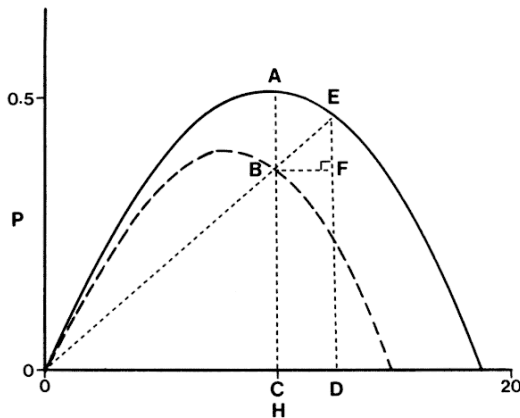


Figure 7: Graphical derivation of the effect of pests (-----) on an empirical productivity (P)/stocking rate (H) curve. See text for explanation. P measures weight gain (kg ha^{-1}); H is stock units ha^{-1} .

Discussion and Conclusions

Graphical consideration of the productivity/stocking rate relationships and analysis of simple herbivore/vegetation interactive models, show that any negative influence on the grazing system displaces the productivity/stocking rate curve downwards and to the left. It follows that the results of such effects will be non-linearly related both to stocking rate and the intensity of the effect. The greater the asymmetry of the productivity/stocking rate curve the greater the non-linearity of the response to changes or perturbations affecting the pasture. Where this non-linearity is pronounced, the presence of any of the above effects therefore sensitises the system both to further increments of the same effect or initial increments of another.

The presence of a second grazing herbivore affects both the productivity and the stability of the grazing system. A herbivore which denudes pasture affects productivity but not stability, although by increasing effective stocking rate it may increase the likelihood of dramatic productivity declines in existing discontinuously stable systems.

The shapes of the damage functions are similar for grazing pests and denuding pests (Fig. 6b), lying between those for foliage-attacking and product-attacking crop pests (Southwood and Norton, 1973); the reduction in proportional losses as stocking rate is

reduced, however, has no obvious crop parallel. The shapes of the functions are strongly dependent on stocking rate, the form of the vegetation growth curve and grazing efficiency of the pest and stock (especially the ratios b/K and a/K). In practice, however, the initial slope is likely to be more important than the non-linearity. This is because pest densities must be averaged over whole farms before assessing their impact on overall animal production, and these average densities are frequently quite low. If so, then within this range the damage functions may be considered approximately linear (Fig. 6b). The effect of grazing efficiency (b) is also less marked at low pest densities (Fig. 6b), so again the pest's behaviour can be approximated by that of the stock (i.e. b assumed equal to a).

In theory at least, stocking rate adjustments provide a way of managing the pest equivalent in many respects to direct control. The correspondence is clear in Fig. 6a, if productivity on the vertical axis is replaced by net revenue (see for example Norton, 1979, Fig. 7). Curve 1 represents no control in both cases. Curve 2 corresponds to insurance through regular, calendar spraying or reducing stocking rate, both reducing the impact of the pest but carrying a constant cost irrespective of pest density. Curve 3 represents monitoring and either spraying when necessary or adjusting stocking rate when necessary; if the cost of monitoring is included, the line would be displaced downward by a small constant amount at all pest densities.

Assessing the impact of pasture pests on farming systems is extremely difficult. Farmland studies (Kain and Atkinson, 1972; Thompson *et al.*, 1985), and simulation (Barlow, 1985a) are obvious alternatives, but a common short cut has been to cost the pests' effect as an equivalent reduction in stocking rate (eg McLaren and Crump, 1969). As the above results make clear, however, this represents a response to pest attack rather than an estimate of its effect, and there is no way of knowing how similar the damage functions are. However, the simple grazing model (Fig. 6b) compares these functions and suggests that it may be appropriate to cost pest effects in terms of a stocking rate reduction, even if the true effect is to reduce per capita productivity at a fixed stocking rate. This will at least give a useful average estimate, though true losses could be slightly greater or significantly less than the estimate depending on the level to which a particular farm is stocked.

The nature of the damage function also bears on the design of field trials to estimate pest impact.

Since, at a fixed stocking rate, losses depend as much on the stocking rate chosen as the pest's effect, and since the relationship between the selected stocking rate and the theoretical optimum will generally be unknown, less equivocal results are likely to be obtained by adjusting stocking rate to maintain per capita productivity. The use of two fixed stocking rates partly overcomes the problem but still leaves the question of extrapolation to a farm situation; carrying capacities are typically higher in small-scale trials. Using a variable stocking rate enables results to be expressed in proportional terms and hence more readily translated to other situations, since the model shows that proportional reductions do not depend on the initial choice of stocking rate so long as per animal production is maintained.

Consideration of pests as 'denuders' as well as 'grazers' has gone some way towards incorporating the range of feeding behaviour exhibited by invertebrates. However, this is still a considerable simplification in at least two respects. One is the interaction between pasture growth rate and damage for patchily distributed invertebrates. Since these are often relatively immobile, the same pest may switch from a localised grazer to a denuder if consumption exceeds growth within a small area and the pasture is thereby destroyed. This is most likely to occur during periods of low herbage growth rates and is exemplified by the increased effect of Argentine stem weevil (*Listronotus bonariensis*) (Kurchel) during summer droughts (Prestidge, van der Zijpp and Badan, 1984). The reverse may also occur, with a denuding pest having effects more akin to a grazing pest as vegetation density increases. Such is the case for porina (Barlow, 1985d). The second type of behaviour not obviously covered is root feeding, by pests such as scarab beetle larvae. These, too, may best be treated as denuding pests. Given that their distribution is frequently aggregated, overall damage over a large area can be measured in terms of the number and size of patches in which density is high enough to destroy the pasture (e.g. Kain, 1975). Again, though, this will depend on pasture growth rate, with the extremes being no damage or denuding rather than the grazing/denuding combination already mentioned.

Finally, three points arise from the analysis which bear on the more general theory of herbivore/plant interactions. The first concerns the extension of a one herbivore/vegetation model to a two herbivore/vegetation one, which this paper considered in the context of an 'intensive' system (i.e. herbivore numbers fixed; Caughley, 1975). What happens in the corresponding 'extensive' situation with herbivore

numbers varying? The two commonly used models of this kind share the same vegetation growth equation with the intensive model described here, but differ in the form of the herbivore population growth expressions. Caughley (1975) refers to these as the 'laissez-faire' and 'interferential' models, and whereas both apply to a single herbivore/vegetation interaction, only the interferential model can be extended to two herbivores. This is because the laissez-faire contravenes the competitive exclusion principle, the performance of each herbivore depending entirely on the quantity of the same resource. For each, there exists only one vegetation equilibrium (i.e. level of V at which H = 0) so coexistence is impossible. The 'interferential' model, on the other hand, yields a herbivore isocline (relating H to V when V = 0) which is a function of both H and V, so at any given level of V both populations can persist at equilibrium. Essentially, this is because the model subsumes a degree of self-regulation within each herbivore population. Not surprisingly, therefore, it forms the basis for the few 'extensive' two consumer/resource models in the literature (e.g. May *et al.*, 1979), though the biology implicit in the model is somewhat unclear (Barlow, 1985b).

Secondly, it appears on theoretical grounds that discontinuous stability may be less widespread in grazing systems with or without pests than Noy-Meir (1978b) indicates. This is because growth curves for pasture now appear to be leftward-peaked rather than symmetrical (see above), which reduces the likelihood of discontinuous stability. Although Noy-Meir considered such a model to be generally discontinuously stable, his example is based on values of 500 and 25,000 kg ha⁻¹ for a and K respectively. The former is reasonable but the latter, deriving from the standardising procedure used, is excessively high. Measurements on New Zealand ryegrass/white clover swards (C.C. Bell, unpublished data) suggest ceiling yields for green matter, on which the model is based, of around 5000-6000 kg ha⁻¹ in spring and 2000 kg ha⁻¹ in winter. Ceiling yield of green leaf, which comprises the majority of sheep intake, is nearer 1500-2000 kg ha⁻¹ (Tainton, 1974), which would greatly reduce the likelihood of discontinuous stability. Moreover, Noy-Meir's criteria (1978b, Table 4) for discontinuity in one of the commonest growth/consumption models of this kind (his Michaelis/inverted exponential (G₃/C₂) model) appear to be incorrect, and the model to be continuously stable over a much wider parameter space than the author suggests. The discontinuous stability in a recent detailed grazing model (Johnson and Parsons, 1983) is

probably due to an unusually abrupt intake function.

Finally, it appears that growth rate variations enhance stability of grazing systems. Since most pastures display both seasonal and yearly variations in growth, this too suggests that discontinuous stability is less likely than simple equilibrium models would imply.

In conclusion, the simple models described here have helped clarify the nature of pest effects in pastures and have suggested typical forms for the damage functions. The models also offer an approximate method for quantifying economic losses from pest attacks and carry practical messages for the design of field trials.

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Wether P=per hectare productivity, H is stocking rate and u, v and a are constants, then, since gross margin per hectare (GM) is simply $hP - jH$ (h = price/unit product, j = variable cost per stock unit), the gross margin/stocking rate curve will have the same shape:

$$GM = (hu-j)H - (vh)H^a$$

Appendix 2: *The proportional effect on animal productivity given a proportional effect on pasture area or pasture consumption rate.*

Appendix I: *The shape of the per hectare gross margin versus stocking rate curve, compared with the productivity versus stocking rate one.*

If the productivity/stocking rate curve is dome-shaped (e.g. Fig. 5b) and approximated by an equation of the form.

$$P=uH-vH^a$$