Application of an Herbivore-Plant Model to Rest-Rotation Grazing Management on Shrub-Steppe Rangeland

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Abstract

A graphical model of a discontinuously stable herbivore-plant system is used to demonstrate analytically relationships between the amount of rest, stocking rate, and seasons of use in rest-rotation livestock grazing management on shrub-grass ranges. All three of these components are important and their interaction determines the system's response. Important points applicable to management are enumerated.

The science of range management is based on an understanding of the interactive effects of plants and herbivores on long-term forage production and range condition. A livestock grazing management system is one of the chief means of manipulating herbivore-plant interactions in efforts to improve the range resource and ensure a sustained yield of goods and services. A variety of grazing management systems have been applied to various ranges (e.g., Anderson 1967; Valentine 1967; Heady 1970; Stoddart et al. 1975), but basically there are three major categories: (1) those based on continuous grazing, (2) those involving some type of deferment, and (3) those involving systematic rotation of the livestock. It is of prime importance that whatever management system is used must be tailored to the specific requirements of the range resource (Anderson 1967).

Rest-rotation grazing management, as championed by Hormay (1970; Hormay and Evanko 1958), involves the use of deferment and rest (''rest'' means that a pasture is not grazed at all in a given year) along with a rotation of livestock from pasture to pasture. Based on the philosophy that plants must be allowed time to recover vigor following defoliation, it typically involves various combinations of resting a pasture for one or more years, deferring grazing until after seed maturity of specified ''key'' species, and season-long grazing. It is intended to promote the vigor and seedling success of forage species by rest and deferment, promote seed planting of forage species by the mechanical action of animal movement following deferment, reduce ill effects of repeated overuse of preferred areas (such as near water) that commonly occur with continuous grazing, and increase animal productivity as a consequence of increasing forage productivity.

Recently it seems that many misconceptions have developed concerning the applicability and successful design of rest-rotation grazing management systems. The need for a more general understanding of the applications of deferred and rest-rotation grazing management has been pointed out by Hyder and Bement (1977). A better understanding of the dynamics of herbivore-plant systems should provide a stronger basis upon which to assess the consequences of a particular grazing management plan.

Considerable attention in the ecological literature has been given to analysis of predator-prey systems. Rosenzweig and MacArthur (1963) were first to show how graphical techniques, supplemented by mathematical analysis of the system behavior near equilibrium points, can be used to study the general stability properties of simple predator-prey systems. In a logical extension of the trophic relationships of predator-prey models, Noy-Meir (1975) has demonstrated a graphical analysis of herbivore (predator)-plant(prey) interactions. He described a simple model of grazing systems and analyzed its stability, seeking answers to the following questions: ''(1) What are the conditions for a specific grazing system (a given animal with a given vegetation) to be stable at a constant 'stocking rate' (animal density)? (2) How does stability change with stocking rate? and (3) What is the relation between productivity, stability, and stocking rate?'' It was found that in terms of system stability, five basic situations, or cases, could be distinguished.

The purpose of the present paper is to extend Noy-Meir's analysis of herbivore-plant systems in general to rest-rotation grazing management of shrub-steppe range in the Great Basin, U.S.A., in particular. Only one of his cases will be considered, that of a discontinuously stable system with two distinct non-zero steady states and liable to extinction. Though the assumptions of such models can rightfully be questioned, there is considerable empirical evidence that their use in range systems is justified (Noy-Meir 1975).

The Model

Analysis of stability is based on changes in vegetation biomass with respect to time:

$$\frac{dV}{dt} = G - C = G(V) - c(V)H,$$

where V=vegetation biomass per unit area, G=plant growth rate (biomass/time), c=consumption (intake) rate per animal, H=herbivore density, and C=consumption rate (by herbivore population at given H) per unit area. Herbivore density is assumed to be held constant at a given stocking level. The reader is referred to Noy-Meir (1975) for discussion of the implicit assumptions and a more detailed explanation of this and other cases.

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The shape of the G(V) and C(V) curves (Fig. 1) determines which of Noy-Meir's cases is appropriate for a given system. The vegetation parameter (V) for livestock grazing systems in the Great Basin represents tall perennial bunchgrasses characteristic of the region. These are species such as bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), needlegrasses (*Stipa* spp.), basin wildrye (*Elymus cinereus*), and Indian ricegrass (*Oryzopsis hymenoides*) (Franklin and Dyrness 1973). Shrubs and other vegetation are not included, and the model does not deal with interspecific competitive relationships among plants. It is assumed that perennial bunchgrasses will respond to the proper sequence of rest and grazing, and analysis is directed at the grass-herbivore interface only.

The general form of the $G(V)$ curve is well established for grasses (Donald 1961; Brougham 1955, 1956). The sigmoidal shape of the CV curve determines that the system is of a discontinuously stable nature. Entirely different results would follow if a curve of another shape were used, and this model would not be appropriate. The sigmoidal shape of the CV curve is appropriate for grasses on a shrub-grass range, because, as grass abundance decreases due to increasing herbivore grazing pressure, the shrub interspaces are depleted first, leaving surviving plants protected under the shrubby species (Tueller and Blackburn 1974); thus it becomes *increasingly* difficult for livestock to "search-out" these remaining individuals. The shrubs are therefore important as a structural feature of the environment in this model. The fact that these grasses are liable to extinction, given a large enough herbivore density (H), is commonly demonstrated by their absence in areas receiving concentrated livestock use, as near water sources (Robertson and Kennedy 1954).

The superimposition of the growth and consumption curves (Fig. 1) demonstrates the system behavior for a given herbivore

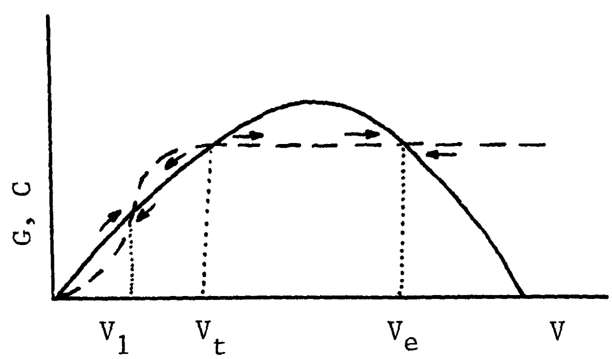

Fig. 1. *Superimposition of* G(V) *(solid line) and* C(V) *(dashed line) curves at given* H; *two equilibrium points* (V_e *and* V_l) *separated by a turning point* (V_t). *Redrawn from Noy-Meir (1975).*

density (H). Intersections of the two curves are points of equilibrium. The direction of vegetation change surrounding an equilibrium point determines whether it is a stable equilibrium (from which small perturbations result in the system returning to the equilibrium point) or an unstable equilibrium (from which small perturbations result in the system moving toward a different equilibrium point). It is seen that there are two stable and one unstable equilibrium points in the present model (Fig. 1). Stable equilibrium points occur at V_1 (low level equilibrium plant biomass) and V_e (high level equilibrium plant biomass). (The intersection at V=0 is of course a third stable equilibrium point, extinction, from which there can be no change.) The unstable equilibrium point occurs at V_t (turning point of plant biomass) and represents a critical threshold where a slight perturbation to the right will move the system to V_e, and a slight perturbation to the left will move the system to V_1. Herbivore productivity at V_1 is lower than at V_t or V_e.

The stability properties of this system may perhaps be more easily visualized with Noy-Meir's mechanical "ball-in-container" analogue (Fig. 2). The ball is at equilibrium in either

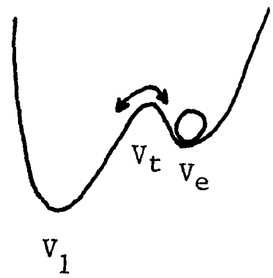

Fig. 2. *A "ball-in-container" analogue to the two steady-states model. Redrawn from Noy-Meir (1975).*

pocket, but sufficient rocking or steady force can move it across V_t, and it will come to rest in the other pocket.

The effects of H can be seen by superimposition of a series of $C(V)$ curves (for different values of H) on the $G(V)$ curve (Fig. 3). The (V,H) values of the intersection of a family of these

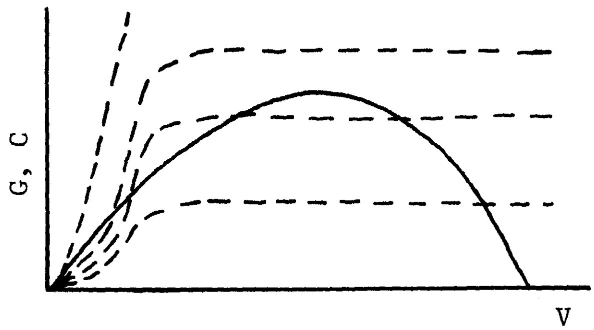

Fig. 3. *Effect of varying herbivore density* H *on the* C(V) *curve (dashed lines). Redrawn from Noy-Meir (1975).*

curves may be determined and plotted (Fig. 4) to provide a graph of the zero-change isocline of the vegetation in the herbivore-vegetation phase plane (Rosenzweig and MacArthur 1963). This graph shows that at low herbivore densities the system will have a single, stable equilibrium point with high

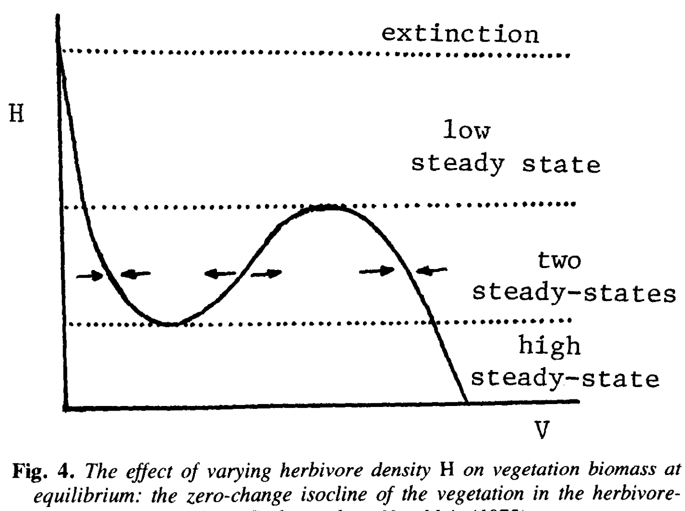

Fig. 4. *The effect of varying herbivore density* H *on vegetation biomass at equilibrium: the zero-change isocline of the vegetation in the herbivore-vegetation phase plane. Redrawn from Noy-Meir (1975).*

plant biomass. As H increases, the system passes through a region of having two steady-states and one turning point (as in Fig. 1) to a region with a single, stable equilibrium point with very low plant biomass, and finally to extinction.

Changes in animal productivity (P) with respect to H can be examined by plotting the values of C against those of H from Figure 3. This is shown in Figure 5. Maintenance (M) is a linear function of H, and net animal productivity is the difference between P and M. Thus the $P(H)$ curve rises in a continuous convex form until maximum animal productivity is reached; but slightly beyond that point steady-state productivity drops suddenly to a much lower level or even to zero. As the point of maximum animal productivity is approached, V decreases toward V_t, and when V and V_t merge, vegetation productivity may drop suddenly to the lower level due to random variability

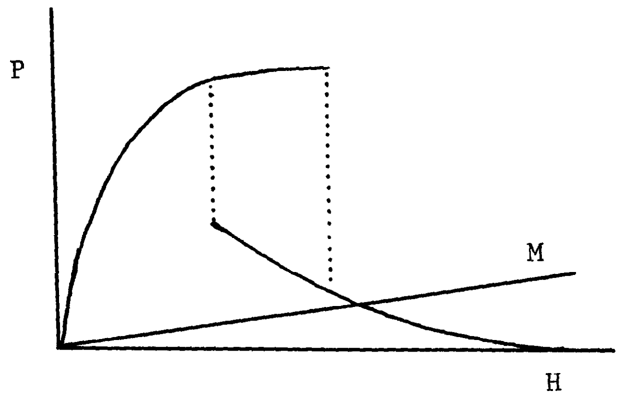

Fig. 5. *Gross herbivore productivity* P *at equilibrium, as a function of herbivore density* H. M *is the cost of maintenance. Redrawn from Noy-Meir (1975).*

alone. Thus Noy-Meir (1975) has pointed out that in such a system "animal productivity may remain very high even when the system is on the verge of a catastrophical collapse. Animal condition is not a sensitive indicator of the state of such a system." Furthermore, he pointed out that within the intermediate range where two levels of productivity are possible, a higher stocking rate will be associated with a higher probability of a transition from high to low relative to a transition from low to high steady-states.

Applications to Rest-Rotation Grazing Management

Analysis of rest-rotation grazing management is not explicit in the model, because the model represents a continuous process. However, the effects of rest-rotation can be assessed by considering the periodic perturbations imposed on the equilibrium point brought about by the alternate years of grazing, deferment, and rest. Noy-Meir (1975) has pointed out that the benefits of rotation over continuous grazing management should be expected to be quite different depending upon which steady-state the system is in. If a continuous grazing system is at the high level equilibrium, the introduction of severe perturbations in the form of a rest-rotation system may be enough to inadvertently push the system past the turning point to the low level equilibrium. On the other hand, if the system is already at the low level equilibrium, the rest-rotation management may be enough to shift the stability to the high level equilibrium. In short, Noy-Meir believed that if the system is already in a high level steady-state, we may only lose by perturbing it; if in the low level steady-state, we may gain; and that if the perturbations are not sufficient to change steady-states, there should be no significant difference between rotational and continuous grazing.

Assuming now that the system is already in the low steady-state (this assumption appears quite reasonable for much of Great Basin rangeland today—e.g., U.S.D.I. Bureau of Land Management 1974; Box et al. 1976), the model can yield insight into questions regarding the importance of the amount of rest, stocking rates, and seasons of use in rest-rotation grazing management systems. These are areas in which many of the misconceptions about rest-rotation grazing management presently lie (Hyder and Bement 1977).

Amount of Rest

Resting a pasture has the effect of temporarily reducing the herbivore density to zero, leaving the change in V with respect to time dependent only upon the $G(V)$ curve:

$$\frac{dV}{dt} = G(V).$$

Thus when grazing pressure is removed from a system at low steady-state, V will always move toward the right (will increase) in the model. The rate at which it increases in a real range system will depend upon the vigor of the grasses at the time the pasture is rested. The longer the rest period, the nearer will V approach V_t. Even if V_t is not reached during a given rest period, however, if grazing pressure between rest periods is not sufficient to return V to V_1 it is possible that V will eventually reach V_t and from there shift to the high level steady-state (V_e). The requirement, of course, is that the amount of rest provided for the vegetation to recover vigor be sufficient to exceed all losses suffered during the grazing periods between rest perods. In terms of the "ball-in-container" analogue (Fig. 2), the rest must be sufficient to eventually rock the ball over V_t to V_e.

According to Hormay (1970), "the key plant in deciding the amount of rest needed is the species that needs the most rest to regain vigor after it has been completely defoliated during the critical green period." Rest periods could be as short as 1 year for Indian ricegrass (Cook and Child 1971) or 14 to 26 months for western wheatgrass (*Agropyron smithii*) (Trlica et al. 1977); but where 6 to 8 years of rest may be required for Idaho fescue and bluebunch wheatgrass (Mueggler 1975), such stringent rest requirements are seldom met. An inadequate rest period will allow V to temporarily increase but will not be sufficient to "rock the ball" to the high level steady-state. Such ranges may look better under a rest-rotation grazing management system, but it is unlikely that management will attain its goal, if that goal is to move the equilibrium to the high level steady-state.

Stocking Rates

Stocking rates during a grazing period determine the force which the herbivore population will exert on the vegetation. In terms of Figure 3, this force is proportional to the difference between the $C(V)$ and $G(V)$ curves and increases with herbivore density. If grazing pressure is sufficient to negate the gains made by vegetation during the rest periods, the system will remain in the low level steady-state. It is also important to note that with a large enough H the vegetation may be forced to extinction, from which point no amount of rest or change in stocking rate can move it.

As demonstrated in Fig. 5, herbivore density is a very critical factor in the productivity of discontinuously stable systems. The greater the value of H, the greater will be the probability of changing from high to low steady-states. This also has major significance for management once the high steady-state has been reached—too great an increase in stocking rate may inadvertently push the system back to low level productivity. This is especially important on desert ranges, where precipitation is so highly variable. It seems to be a common misconception that stocking rate is not an important factor in rest-rotation grazing management systems (Hyder and Bement 1977).

Seasons of Use

The major effect of seasons of use in this model is that a later turnout date will result in less grazing pressure during the growing season than will an earlier turnout date for a given stocking rate (animal density). Seasons of use thus affect grazing pressure, and their effects on the system are similar to those of stocking rate. At a given herbivore density, the amount of green biomass consumed will increase with the length of time that the grazing period extends into the growing season. However, the response of plants to grazing varies greatly seasonally. Generally, plants are most sensitive to grazing during the period of maximum growth and corresponding minimum carbohydrate reserves (Cook and Stoddart 1963; Donart and Cook 1970; Cook and Child 1971; Krall et al. 1971); but this is also the time when they are of greatest forage value to livestock (Hormay 1970). Consequently, an optimal combination of seasons of use with stocking rates should be sought.

Summary and Conclusions

A highly simplified model of an herbivore-plant system has been used to demonstrate some general concepts applicable to rest-rotation grazing mangement on shrub-steppe ranges. Although it is far from representing a complete picture of a rangeland grazing system, it is useful in demonstrating several important, but frequently misunderstood, relationships involving amounts of rest, stocking rates, and seasons of use, and their relation to system stability and productivity. The important points applicable to management can be listed as follows:

1) In discontinuously stable systems, herbivore productivity may remain high even when the system is one the verge of collapse. Animal condition is therefore a poor indicator of the state of such a system.

2) Given adequate rest and the proper grazing treatment, a high level equilibrium may be reached where vegetation biomass and herbivore productivity are much greater than was previously possible at a lower level of system stability.

3) The amount of rest required to effect a change from low to high steady-states is directly related to the herbivore grazing pressure.

4) Stocking rates have a direct bearing on the magnitude of herbivore grazing pressure. Low stocking rates will favor a change from low to high steady states and will maintain a high level equilibrium. Conversely, high stocking rates will favor a change from high to low steady-states and will maintain a low level equilibrium. It is conceivable that with a high enough stocking rate, the system may be forced from a low level equilibrium point to extinction.

5) Seasons of use also have a direct bearing on the magnitude of herbivore grazing pressure. Later turnout dates will result in less grazing pressure during the growing season than will earlier turnout dates for a given stocking rate (herbivore density). Response of plants to grazing and quality of forage vary seasonally, however, and the optimal combination of stocking rate and seasons of use must be sought for a given herbivore grazing pressure.

Therefore, the amount of rest, stocking rate, and seasons of use are all important and interrelated components of a rest-rotation grazing management plan. The optimal mix of all three is what is considered tailoring the grazing management to the range resource. With proper management, discontinuously stable herbivore-plant systems have the potential for stability at a relatively high level of production and vegetation biomass. Once there, fine tuning of herbivore productivity must continue to be based on vegetation response.

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