

## 7

## Plant-Herbivore Systems

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## 7.1 Introduction

'Herbivore' is a catch-all word, encompassing not only cows, horses, sheep and their wild relatives, but also phytophagous insects, and beasts as different as giant tortoises, slugs and grouse; *Daphnia* and protozoa in ponds; limpets and urchins on the sea-shore and teeming zooplankton in the open ocean. They graze on food ranging from blue-green algae to beech leaves, and *Lemna* to *Laminaria*. Not surprisingly there is no such thing as a typical herbivore. At the risk of enraging vertebrate ecologists and range managers, who use 'grazing' in the strict sense of 'eating grass and herbs', we have used the word to mean 'eating any kind of plant or part of a plant, by any kind of animal'.

In order to make the chapter manageable, we have focussed on two main taxa: phytophagous insects because there are so many of them, and mammalian herbivores because what they lack in species they more than make up for in economic importance, impact on ecosystems, and aesthetics. The main insect groups feeding on plants are described by Southwood (1973): the total number of species involved is unknown, but there are roughly 120,000 different species of caterpillars in just the one order Lepidoptera for example, compared with a paltry 212 ungulates (Proboscidea, Perrissodactyla and Artiodactyla). Even the rodents muster less than 2000 species. Phytophagous insects and mammals aside, our examples are an eclectic selection from the ark, guided more by expediency than the gathering of a representative zoo.

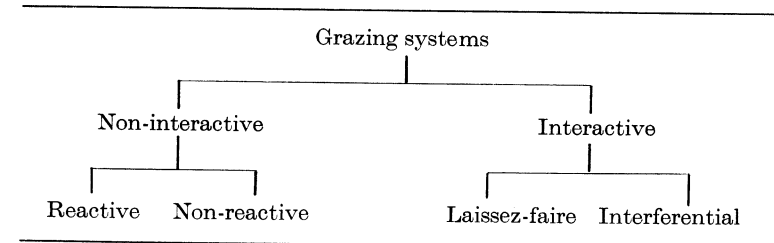
The chapter opens (section 7.2) by providing a classification of grazing systems, to which examples can be assigned with varying degrees of confidence (section 7.3-7.4). Lotka-Volterra models provide the underlying theoretical frame, building directly on classical predator-prey interactions (chapter 5). This has been done deliberately, even though we know plants and their herbivores are different in many ways from predators and prey. Unfortunately the empirical data are lacking

to build more realistic general models. Instead we have chosen to work from a familiar base, pointing to obvious flaws and elaborations as the chapter progresses. Eventually, we would hope to be able to abandon the base altogether. The most interesting elaborations and the most promising framework on which to construct the next generation of models are dealt with in section 7.5. Perhaps more than any other chapter we would expect this one to look totally different in 10 years time.

## 7.2 A classification of grazing systems

Table 7.1 is a classification of grazing systems in which the primary division is made according to Monro's (1967) dichotomy: between those systems in which the herbivores influence the amount of food available

**Table 7.1.** A classification of relationships between plants and herbivores.



to themselves and subsequent generations, and those where they do not. The first is an 'interactive system', the second 'non-interactive'.

The essence of a *non-interactive system* lies in the herbivore's inability to influence the rate at which its resources are renewed. It subdivides uneasily into 'reactive systems' where the rate of increase of herbivores reacts to the rate at which plant material is renewed (there being no reciprocal reaction), and 'non-reactive systems' in which the herbivores increase at a rate largely independent of the parameters of plant growth.

In an *interactive system* the herbivores do influence the rate of renewal of the vegetation, which in turn influences the rate of increase of the animals: the two components interact. This class divides again into 'laissez-faire systems' in which the herbivores do not interfere with

each other's feeding activities, and 'interferential systems' in which an animal may reduce the ability of another to obtain food that would otherwise be available to it. These two systems have different dynamics.

### 7.3 The dynamics of grazing systems: non-interactive systems

#### 7.3.1 Theory and examples of reactive systems

This, our first and simplest example, is also, not unreasonably, the most unrealistic.

If the rate of renewal of the food of the herbivores,  $g$ , is independent of the standing crop of plants,  $V$ , food availability changes as

$$dV/dt = g. \quad (7.1)$$

When a herbivore population of size  $H$  feeds on these plants, with each herbivore eating at a constant rate  $c$ , the change in  $V$  might become

$$dV/dt = g - cH. \quad (7.2)$$

Alternatively, if each herbivore has a maximum rate of intake,  $c$ , which declines as the food supply is thinned out, then

$$dV/dt = g - cH(1 - \exp(-dV)). \quad (7.3)$$

Real field examples approximating to such a system are extremely rare. In the deserts of the south-western United States, the larvae of several species of *Drosophila* feed on cacti. Strictly they are not herbivores but eat yeasts which live in rot-pockets in the cactus (Fellows and Reed, 1972; Starmer *et al.*, 1976). The adults however share many of the problems of host-plant location and exploitation confronting real insect-herbivores, sufficient for us to make them honorary members and give some biological flesh to the bones of an otherwise abstract argument. To avoid misunderstanding, we are here only concerned with what might happen to the cactus-*Drosophila* interaction over a reasonably large area of the desert. Within each rot-pocket larvae and yeast are highly interactive.

Rot-pockets are generated at a rate  $g$ , quite independently of the rate at which the *Drosophila* exploit them; generally, the stem of a cactus will undergo some injury (e.g. freezing), rendering the damaged tissue vulnerable to infection. The *Drosophila*'s dynamics can be

pictured as follows. If  $b$  is defined as the rate of intake sufficient to maintain a herbivore and allow its replacement in the next generation, then the proportion of available food used for maintenance is  $bH/g$ , leaving  $(1 - bH/g)$  that can be channelled into generating an increase of herbivores. With rising  $H$ , the herbivores' rate of increase slows progressively until finally all the food is utilized for maintenance, and the population stabilizes at  $H = g/b = K$ . Hence the herbivore population grows as

$$dH/dt = rH(1 - bH/g). \quad (7.4a)$$

Here  $r$  is the herbivore's intrinsic rate of increase, the rate at which it would increase in that environment if no resource were limiting. Substituting  $K$  for  $g/b$  turns the equation into the common form describing logistic growth, eq. (2.3):

$$dH/dt = rH(1 - H/K). \quad (7.4b)$$

The assumptions underlying this model can therefore be summarized as the characteristics a population must possess if it is to grow logistically:

- (a) A population's resources are renewed at a constant rate, independent of both the standing crop of the resource and the standing crop of the population, the population having no influence over the amount of resource available to the next generation.
- (b) The members of the population have insatiable appetites.
- (c) Rate of increase is a linear function of average food intake per head.
- (d) There is no lag between cause and effect.

Of these four conditions for logistic growth only the first is critical.

How clearly the cactus-living *Drosophila* conform to these assumptions is unknown, but we would be surprised if their large-scale dynamics were not roughly logistic. Gause's (1934) classical laboratory populations of *Paramecium*, 'grazing' on the bacterium '*Bacillus pyocyaneus*' (= *Pseudomonas aeruginosa*) do conform to these major assumptions, and pleasingly they behave more or less as predicted (Fig. 8.4a). At the beginning of each experiment Gause placed twenty *Paramecium* in a tube and guaranteed conformity to eq. (7.1) by adding a constant quantity of *Bacillus* every day. Gause (1934), Kostitzin (1939) and Andrewartha and Birch (1954) all fit logistics to the data.

We had ulterior motives for developing the conditions for logistic growth in some detail, because in subsequent sections we use a logistic equation to model the growth in biomass of plant (rather than herbivore)

populations. This does not mean we necessarily believe this equation describes how most plant populations behave, but rather because it provides a standard of ideal behaviour against which reality can be judged and measured (Harper, 1977). To the extent that plants cannot influence the rate of input of key resources, particularly sunlight and water, to the next generation, our use of the logistic is justified and has some empirical support (Brougham, 1955; Clatworthy and Harper, 1962; Davidson and Donald, 1958; Ikusima *et al.*, 1955), though even the simplest of systems do not always conform (Laws, 1980: see also 7.4.1). Unfortunately data on plant population dynamics are too sparse to justify a general analysis of plant-herbivore models in which the growth of the vegetation is markedly non-logistic. Providing plant biomass approaches an ungrazed asymptote along any roughly 'S' shaped curve, our models will not be seriously in error.

### 7.3.2 *Phytophagous insects: reactive and non-reactive examples*

Figure 7.1 summarizes population data for the herbivorous insects on two species of plants, namely bracken fern (*Pteridium aquilinum*) and the grass *Holcus mollis* (Lawton and McNeill, 1979). The insects on both plants share two features typical of many others (see Lawton and McNeill, 1979 for a review). First a small proportion of species may become temporarily very abundant and, when they do, inflict serious damage upon their hosts. Aphids (*Holcaphis*) and thrips (*Aptinothrips*) on *Holcus*, and broom moth, *Ceramica pisi*, on bracken are good examples. (Others are provided by Dixon, 1971a, b; Newbury, 1980a, b; and Tilden, 1951.) Such species clearly belong in the 'Interactive' category and will be returned to later (sections 7.4.2, 7.4.3 and 7.5.1). Second, the majority of species are never very abundant: most in fact are rare or very rare relative to the abundance of their food plants. Table 9.3 makes the same point in a different way. We assume most (though certainly not all) of these rare species have little or no impact upon the dynamics of their hosts (see Harris, 1973), and hence are non-interactive.

Three hypotheses may account for the rarity of most phytophagous insects most of the time:

(1) Contrary to superficial appearances, large parts of the plant are quite unsuitable as food, either because of a low nutritional status (e.g. Dixon, 1970; McNeill, 1973; McNeill and Southwood, 1978; White, 1969); or because they are chemically defended in some way (Feeny,

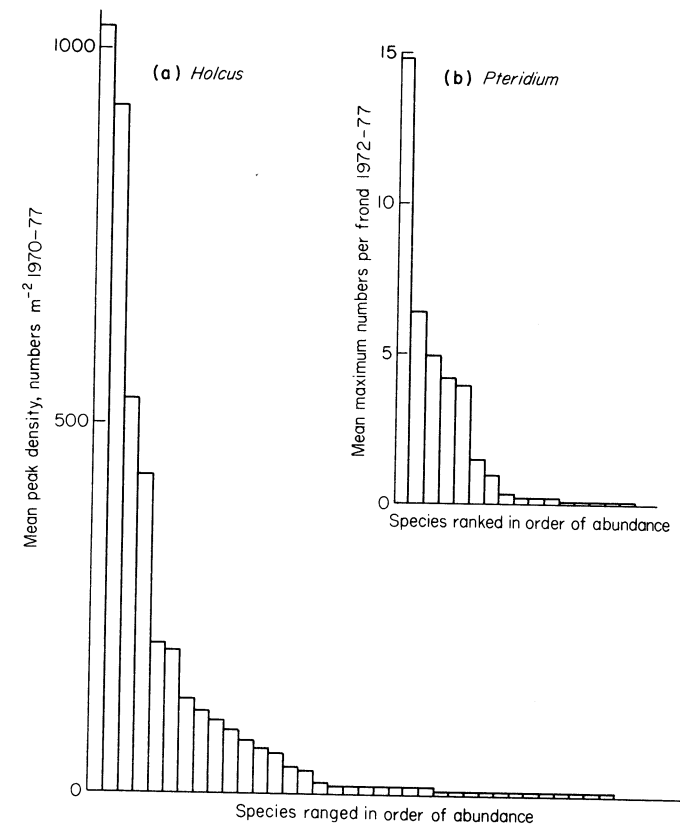


Fig. 7.1. Mean maximum densities of phytophagous insects on (a) the grass *Holcus mollis* and (b) the fern *Pteridium aquilinum* (Lawton and McNeill, 1979). Most species are rare most of the time.

1976; Rhoades and Cates, 1976); physically defended by the microscopic equivalent of thorns (Pillemer and Tingey, 1976; Ratheke and Poole, 1975); or simply too large, too small or too tough to exploit properly (Dixon and Logan, 1973; Whitham, 1978). Southwood (1973) reviews many of these problems. Populations in this category are, despite appearances, food-limited (van Emden and Way, 1973) and hence lie towards the reactive end of the non-interactive spectrum.

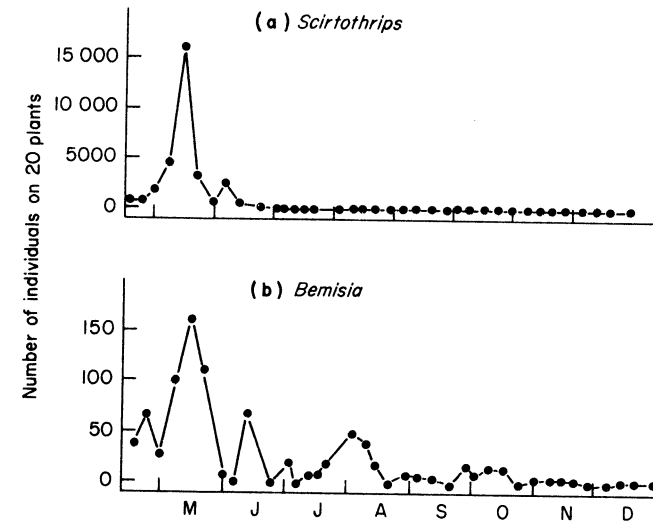
(2) Many species are kept rare most of the time through the vagaries and harshness of their environment. Safe sites are either highly localized and/or unpredictable in space, or conditions are rarely good enough for long enough for species to bump against the ceiling of food limitation (Andrewartha, 1970; Andrewartha and Birch, 1954; Thompson *et al.*,

1976; Whittaker *et al.*, 1979). By definition, such species are non-interactive over most of their habitat, most of the time. About 25 years ago, ecologists debated at great length whether populations could exist in the complete absence of density-dependent controls (which *in extremum* is what is implied by this hypothesis). Probably the best known example is the controversy surrounding the dynamics of *Thrips imaginis*, which feeds on sap and pollen (Andrewartha and Birch, 1954; Varley, 1963; Varley *et al.*, 1973). Irrespective of whether or not there are density-dependent controls in this population (there are) it provides a good example of a predominantly non-interactive herbivore.

(3) Natural enemies, particularly insect predators and parasitoids (chapters 5 and 6), or birds (Holmes *et al.*, 1979), true parasites and diseases (see chapter 14) play a key role in keeping many phytophagous insects rare relative to their food resources (and see Hairston *et al.*, 1960). Where natural enemies are very effective, food-limitation may again be negligible (Fig. 7.13). Successful biological control of former insect pests (Beddington *et al.*, 1978; Fig. 9, chapter 6; see also chapter 15) has transformed some highly interactive grazing systems into deceptively peaceful, non-interactive non-reactive states.

Species of insects from one habitat and food plant may between them span the full gambit of possible behaviours (Fig. 7.2). A summary of life-tables for phytophagous insects is given in Table 7.2. For many of these species, natural enemies are clearly important controlling agents; others appear to be controlled by food limitation, or by disease; and in still others it has not been possible to demonstrate any density dependence. As a sample of the world's phytophagous insects, Table 7.2 is pathetically small, but it shows clearly that anything can, and does, happen. Some species are interactive: most appear to be non-interactive, and within the latter category we expect to see both reactive (food limited) and non-reactive examples.

In parentheses, note that exactly the same phenomena influence the interaction of other herbivores with their food-plants. (1) Grazing mammals are highly selective in what they eat (Freeland and Janzen, 1974; Leuthold, 1977) and pond snail populations (*Limnaea*) respond vigorously to small quantities of high quality food (Eisenberg, 1970). (2) A regular annual dry season depresses ungulate and small mammal populations in the Serengeti well below their apparent food supply during the rest of the year (Sinclair, 1975); and shortage of shady sites, safe from overheating, is a severe problem for giant tortoises on Aldabra (Swingland and Coe, 1979). Finally, (3) predators may tem-



**Fig. 7.2.** The insects feeding on a small isolated plot of Cassava (*Manihot esculenta*) illustrate three alternative dynamical patterns (Samways, 1979). (a) The thrip *Scirtothrips manihoti* feeds on the upper leaves and buds. The population increased exponentially in the spring until the onset of lower temperatures, rain and heavy dew caused high density independent mortality and a rapid decline (hypothesis (2), p. 137). (b) The whitefly *Bemisia tuberculata* feeds on the lower and middle leaves. Predation and parasitism were negligible, yet the population never became very abundant 'apparently due to some lack of preference' (hypothesis (1), p. 136). (c) Not illustrated. The moth *Erinnys ello* also colonized the plant, but 83 per cent of eggs were parasitized by *Trichogramma*; the caterpillars were also parasitized by two hymenoptera and a tachinid, *Euphorocera*. As a result the moth remained extremely rare (hypothesis (3), p. 138).

porarily limit small mammal populations during the 'lows' of a population cycle (Pearson, 1966); or permanently in the case of sea otters and their sea urchin prey (Estes and Palmisano, 1974). Disease (rinderpest) can make terrible inroads into ungulate populations (Delany and Happold, 1979).

Obviously, the dichotomy between reactive and non-reactive species, and the larger one between interactive and non-interactive systems is one of convenience. Some food limitation is inevitable unless natural enemies or climate markedly depress the population, and some effects on the host plant must follow if the herbivores themselves experience food limitation. Thus, despite density-dependent pupal predation (Table 7.2), winter moth caterpillars become sufficiently abundant in

**Table 7.2.** Summary of main density-dependent controlling factors operating on populations of phytophagous insects, revealed by life-table studies (Varley *et al.*, 1973). Data are from Podoler and Rogers (1975), supplemented by Stubbs (1977), and other sources given in the table.

Species	Density dependent mortalities, discovered by original authors, or by subsequent analysis (see references for details).
Parasitism, Predation and Disease	
West Indian cane fly (Diptera) <i>Saccharosydne saccharivora</i> : '2 Dundas' 'D-Piece'	Egg parasitism by <i>Tetrastichus</i> Parasitism of early nymphs by <i>Stenocranophilus</i>
Yew gall midge (Diptera) <i>Taxomyia taxi</i>	None identified: the life-cycle of this herbivore is very complex, and parasitism by <i>Mesopolobus</i> may be density-dependent in one-year life cycle galls (Redfern and Cameron, 1978).
Cabbage root fly (Diptera) <i>Erioischia brassicae</i>	Pupal parasitism by <i>Aleochara</i> and some predation on pupae.
Broom beetle (Coleoptera) <i>Phytodecta olivacea</i>	None identified: soil mortality due to predation up to emergence of adults in autumn may be density dependent.
Spring usher (Lepidoptera) <i>Erannis leucophaearia</i>	Parasitism and predation (Stubbs, 1977).
Pine looper (Lepidoptera) <i>Bupalus piniarius</i>	Larval mortality due mainly to parasitism by <i>Eucarcelia</i> and <i>Poecilostictus</i> . Infectious disease also important (Anderson and May, 1980, 1981).
Mottled umber (Lepidoptera) <i>Erannis decemlineata</i>	Parasitism and predation (Stubbs, 1977).
Winter moth (Lepidoptera) <i>Operophtera brumata</i> : England	Pupal predation, by carabid and staphylinid beetles and small mammals. Infectious disease also important (Anderson and May, 1981).
	Canada
Grey larch moth (Lepidoptera) <i>Zeiraphera diniana</i>	None identified, but parasitism of caterpillars by <i>Cyzenis</i> (and <i>Agrypon</i> ?) is strongly regulatory (Hassell, 1978; Beddington <i>et al.</i> , 1978). None identified: parasites or predators on eggs or pupae may be a 'major cause' (delayed density-dependence) of cycles (Varley and Gradwell, 1970). More likely, the cycles are driven by infectious disease (Anderson and May, 1980, 1981).
Black-headed bud worm (Lepidoptera) <i>Acleris variana</i>	None identified: parasites or predators on eggs or pupae may be a 'major cause' (delayed density-dependence) of cycles (Varley and

Table 7.2 (continued)

	Gradwell, 1970). More likely, the cycles are driven by infectious disease (Anderson and May, 1980, 1981).
	Competition for Food
Grass mirid (Heteroptera) <i>Leptoterna dolabrata</i>	Competition for high nitrogen feeding sites by adults.
Colorado beetle (Coleoptera) <i>Leptinotarsa decemlineata</i>	Starvation of older larvae through food shortage. Parasitism of pupae by <i>Doryphorophaga</i> may also be density dependent (Stubbs, 1977).
Cinnabar moth (Lepidoptera) <i>Tyria jacobaeae</i>	Death of caterpillars from starvation, and delayed density-dependent reduction in adult fecundity (Dempster, 1975).
	Other
Large copper (Lepidoptera) <i>Lycaena dispar</i>	Decrease in adult fecundity (Stubbs, 1977).
Frit fly (Diptera) <i>Oscinella frit</i>	None identified, but adult mortality, seasonal migration and variation in fecundity appear to be density dependent in combination. Cause unknown.
Tea moth (Lepidoptera) <i>Andracea bipunctata</i>	None identified (Banerjee, 1979).
Olive scale (Homoptera) <i>Parlatoria oleae</i> : Hills valley	None identified.
	Herndon
	None identified.

some springs to defoliate the oak trees (*Quercus*) on which they feed. Defoliation impairs the growth of young oaks, and could greatly influence the outcome of competition between trees struggling for dominance (Gradwell, 1974), just as periodic outbreaks of tent caterpillars (*Malacosoma*) favour the main understory species (*Abies balsamea*) at the expense of the defoliated dominant, *Populus tremuloides* (Harper, 1977). This leads us naturally into a consideration of interactive systems.

#### 7.4 The dynamics of grazing systems: interactive systems

One of the commonest grazing systems is that in which the rate of change of herbivores is a function of plant density, and the rate of change of plants is a function of herbivore density. The two components interact. Formally, the 'plant density' in this context is the

quantity of vegetation per unit area which is available both for consumption by animals and for producing plant growth (Noy-Meir, 1975).

A model of this system must include several parameters: usually two for plant growth, two for grazing pressure and two or three for the growth of the herbivore population. Here is a representative set of parameters\* for such a model:

- $r_1$  = the intrinsic rate of increase of plants,
- $K$  = maximum ungrazed plant density, or biomass,
- $c_1$  = maximum rate of food intake per herbivore,
- $d_1$  = grazing (searching) efficiency of the herbivore when vegetation is sparse,
- $a$  = rate at which herbivores decline when the vegetation is burned out or grazed flat,
- $c_2$  = rate at which this decline is ameliorated at high plant density,
- $d_2$  = demographic efficiency of the herbivore; its ability to multiply when vegetation is sparse.

A number of choices are available to depict the relationship between plant density and rate of food intake per herbivore (the functional response), and between plant density and rate of increase of the herbivore (the numerical response): see Table 5.1. We have used simple functions that rise with increasing plant density, and saturate when food is abundant. The numerical response used here ignores the effect of 'underpopulation', that is, reduced fecundity at low density reflecting the difficulty of finding a mate when mates are scarce. This is a deliberate simplification. Underpopulation has not, to our knowledge, been identified for any herbivore, vertebrate or invertebrate, although it may sometimes occur.

#### 7.4.1 *Laissez-faire systems*

In a laissez-faire interactive system the herbivores do not interfere with each other's search for food. Non-territorial ungulates provide a good example of this kind of grazing behaviour. Noy-Meir (1975) explored by graphic analysis the theoretical implications of holding ungulates at

\* In particularizing from the general prey-predator system of Chapter 5, to the plant-herbivore system of this chapter, the symbol for the prey population,  $N$ , has already been replaced by  $V$  for vegetation, and the symbol for the predator population,  $P$ , by  $H$  for herbivore. Similarly, in what follows there is no attempt to keep the symbols for the various parameters precisely congruent with those used in Chapters 5 and 6 (e.g., those in Table 5.1).

an arbitrary constant density, as in farming, and Caughley (1976) looked at the properties of a system containing wild ungulates hunted by man. To keep it short and simple, the present discussion is limited almost entirely to systems in which wild ungulates range free of persecution.

May (1975a, and section 5.2) has summarized the different ways in which this system can be modelled, and he has emphasized that the qualitative behaviour of the model is insensitive to the details of its construction. Depending on the values of its parameters, the system may be characterized by a stable equilibrium point, or by a stable limit cycle, whose amplitude may be so severe as to produce extinction. Of the many available, one model will suffice to sketch in the outlines of this system:

$$dV/dt = r_1V(1 - V/K) - c_1H[1 - \exp(-d_1V)], \quad (7.5)$$

$$dH/dt = H\{-a + c_2[1 - \exp(-d_2V)]\}. \quad (7.6)$$

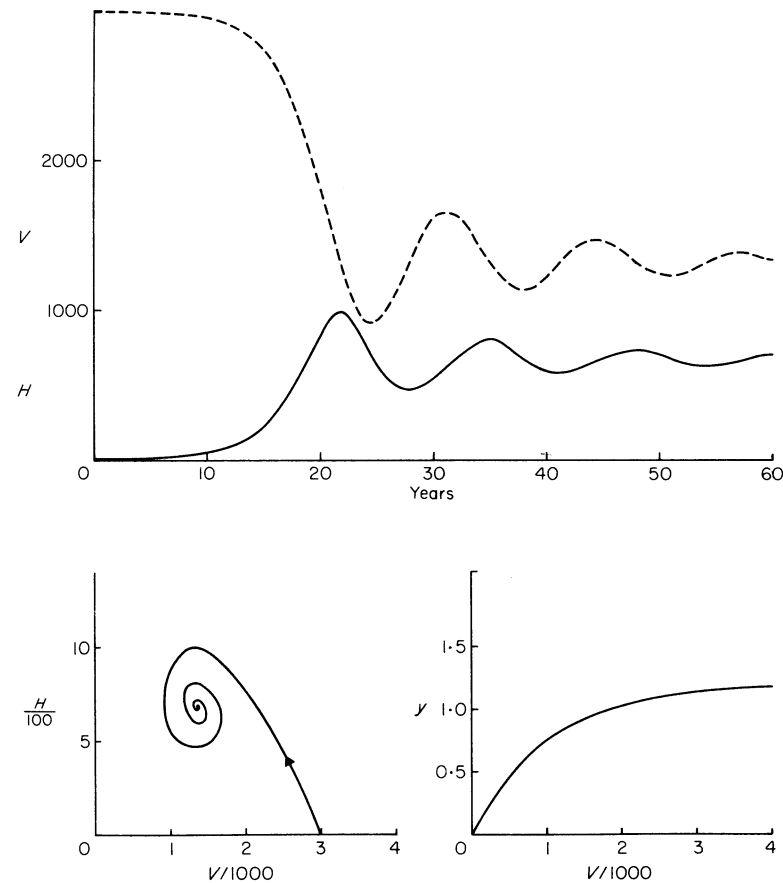
The symbols are as defined above.

The first equation expresses the rate of change of vegetation by two terms, the first depicting logistic growth and the second the rate of grazing. The functional response of diet to plant density is in Ivlev (1961) form; see form (iv) of Table 5.1. Equation (7.6) summarizes the rate of change of herbivores,  $H$ , in terms of their intrinsic ability to multiply, as modified by the availability of food. Herbivores can increase at a maximum rate of  $\{-a + c_2[1 - \exp(-d_2K)]\}$ , which in most circumstances will equal their intrinsic rate of increase,  $r_2$  ( $r_2 = c_2 - a$ ), because at high plant density the term inside the square brackets will tend to unity.

Before exploring the applicability of this model to real grazing systems, we will examine briefly the mathematical properties of a system conforming to these rules. Figure 7.3 shows the growth of a population of herbivores, and the resultant changes in plant density, as the two spiral towards their mutual equilibrium point. For this illustration, the parameters were set at

$$\begin{array}{ll} r_1 = 0.8 & a = 1.1 \\ K = 3000 & c_2 = 1.5 \\ c_1 = 1.2 & d_2 = 0.001. \\ d_1 = 0.001 & \end{array}$$

Although the example is imaginary it can be thought of, without contradicting current knowledge, as white-tailed deer colonizing a mosaic



**Fig. 7.3.** Model of the trend of vegetation ( $V$ ) and herbivores ( $H$ ) during an ungulate eruption. Intake ( $y$ ) of vegetation per herbivore is graphed against density of vegetation.

of grassland and forest. Wildlife managers will recognize the growth curve as a deer eruption. The model has an equilibrium at

$$V^* = (1/d_2) \ln [c_2/(c_2 - a)], \quad (7.7)$$

and

$$H^* = \frac{r_1 V^*(1 - V^*/K)}{c_1[1 - \exp(-d_1 V^*)]}. \quad (7.8)$$

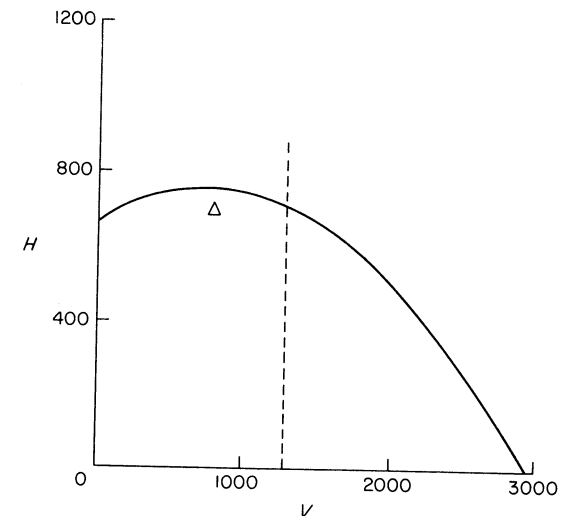
For the parameter values catalogued above, and illustrated in Fig. 7.3, the equilibria are  $V^* = 1300$  and  $H^* = 670$ . Let  $x = d_1 V^*$ : then, depending on the specific parameter values, this equilibrium will be

stable if

$$K < V^* (2e^x - 2 - x)/(e^x - 1 - x) \quad (7.9)$$

or, if not, it will be the focus of a stable limit cycle. We can arrive at this conclusion by applying the graphic methods of Rosenzweig and MacArthur (1963). There will be one or more values of  $V$  at which  $dV/dt = 0$  when  $H$  is held constant at some arbitrary value. The points may represent maxima or minima of cycles, or stable equilibrium. They can be plotted on a graph of  $H$  against  $V$ . If this procedure were followed for every possible value of  $H$ , the resultant points would fall along a curve, the zero 'isocline' of  $V$ . The form of this curve, expressing  $H$  as a function of  $V$ , clearly is given by eq. (7.8). Similarly, there is a set of points at which  $dH/dt = 0$  when  $V$  is held constant. This isocline of herbivores is an inverted  $T$ , the crossbar coinciding with the uninteresting instance of  $H = 0$ , and the vertical rising from the  $V$  axis at the value  $V^*$  given by eq. (7.7). Figure 7.4 gives the zero isoclines of  $V$  and  $H$  for the numerical example above.

The salient feature is whether the position of the isocline of  $H$  is to the right of the highest point, indicated by a triangle, of the  $V$  isocline. That is a necessary and sufficient condition for point-stability of this model (Rosenzweig, 1971; Gilpin, 1972). The system's equilibrium



**Fig. 7.4.** Graph of the zero isocline for vegetation (the curve) and the zero isocline for herbivores (vertical line) for the 'white-tailed deer' model: the triangle indicates the peak of the  $V$  isocline.

point [the  $V^*$ ,  $H^*$  of eqs. (7.7) and (7.8)] of course lies at the intersection of the two isoclines. If the equilibrium point lies to the left of the hump, the system will cycle.

For relatively large values of  $d_1V^*$ , the stability condition eq. (7.9) simplifies to

$$K < 2V^*. \quad (7.10)$$

This approximation is within 2 per cent for  $d_1V^* > 5$ . In this form the biological implications are more apparent: a system of a vegetation and a population of efficient herbivores has oscillatory behaviour if grazing pressure tends to hold the standing crop of vegetation below half that of its ungrazed state.

This simple conclusion requires two important qualifications. First, it applies only to laissez-faire systems. Second, it describes what happens in a spatially uniform world, and the food of most herbivores is very far from being uniformly distributed; witness the spectacular migrations of ungulates across the Serengeti (Delany and Hapgood, 1979), the responses of the parsnip web worm *Depressaria pastinacella* to clumps of wild parsnip *Pastinaca sativa* (Thompson, 1978), and the patchy distribution of *Daphnia* and algae in lakes (Hebert, 1978). Just as the dynamics of predator-prey interactions are markedly changed by the inclusion of spatial heterogeneity (chapter 6), so too are herbivore-plant interactions, although the problem has received much less attention. We return to the question of spatial heterogeneity in section 7.4.3. A cautious, qualitative interpretation of eq. (7.10) therefore reduces to: heavy grazing leads to oscillations, and no more.

The laissez-faire model is at its best as a summary of the interaction of a population of predominantly non-migratory ungulates and their food supply. For appropriate parameter values the trajectory of an ungulate population increasing from minimal density while grazing vegetation initially at density  $K$  follows an eruption to a peak, a crash, and a 'stabilization' around an equilibrium level well below the peak density (Caughley, 1970). Figure 7.5 shows the eruption of sheep introduced into western New South Wales. The parallel between this trajectory and that simulated in Fig. 7.3 is immediately apparent. Despite its undoubted limitations the model captures the essence of the interaction remarkably well.

Ungulate populations are also prone to erupt when the plant-herbivore system is disturbed. Because the herbivores do not start their upswing from minimal density, and because the vegetation is not

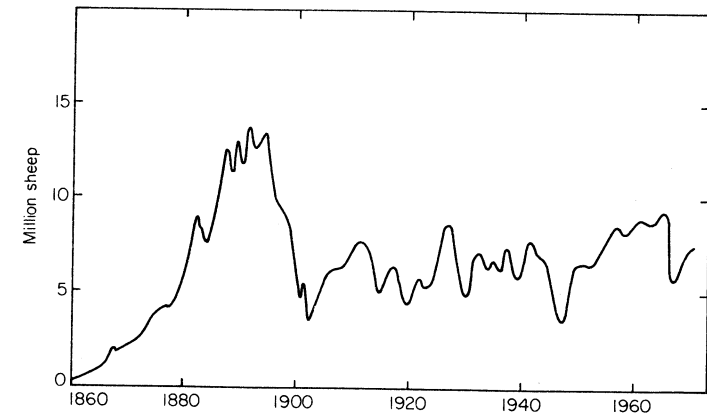


Fig. 7.5. An ungulate eruption: the trend of sheep numbers in the Western Divisions of New South Wales between 1860 and 1972. Data from Butlin (1962) and N.S.W. Yearbooks (1956-1972).

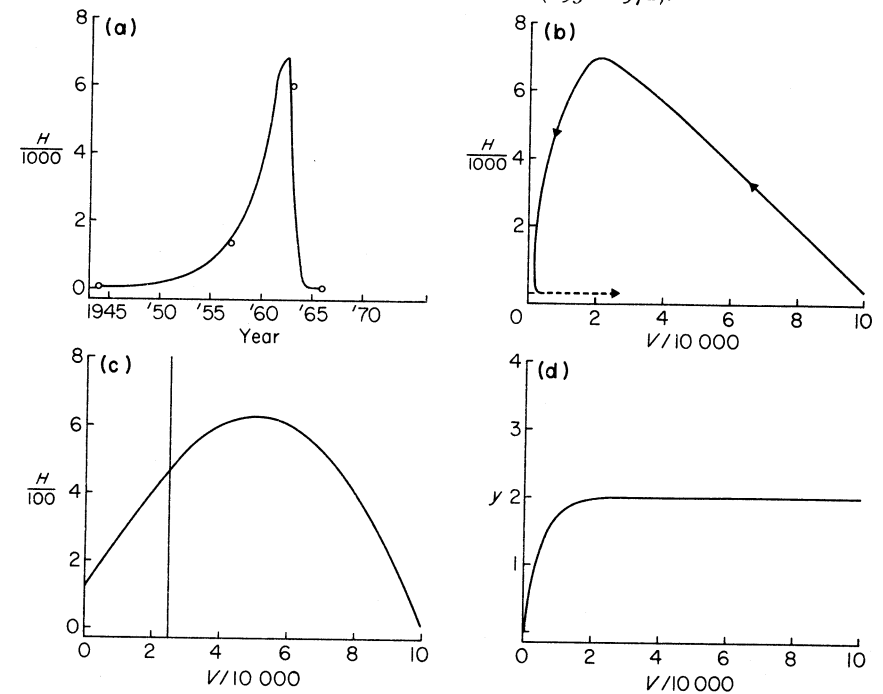


Fig. 7.6. A reindeer population in trouble. Graph (a) is a trajectory fitted by the laissez-faire model to Klein's (1968) estimates of numbers on St. Matthew Island. Graph (b) shows the same trajectory as a plot of herbivores ( $H$ ) against vegetation ( $V$ ); graph (c) shows the zero isoclines for herbivores (vertical line) and vegetation (curve), and graph (d) is intake ( $y$ ) per head against density of vegetation.



at its  $K$  level, these 'sub-eruptions' are not as spectacular as that of Fig. 7.5. They are, however, much more common. Leopold *et al.* (1947) reported over a hundred for deer populations in the United States between 1900 and 1945.

Probably the most spectacular full-scale eruption on record is that of reindeer introduced onto St. Matthew Island in the Bering Sea. Figure 7.6 gives the available estimates of population size (Klein, 1968), to which a trajectory was fitted by eqs. (7.5) and (7.6); see Caughley (1976). The parameter values were guessed rather than estimated. As shown in Fig. 7.6c the intersection of zero isoclines is to the left of the hump, indicating that the system has no stable equilibrium point, and therefore that the reindeer numbers will oscillate cyclically (in this case violently, and probably to extinction).

Equations (7.5) and (7.6) also pass as reasonably good caricatures of coupled zooplankton-phytoplankton interactions. *Daphnia* are typical planktonic grazers, exploiting various species of algae in the upper waters (epilimnia) of lakes and ponds. In permanent water-bodies in temperate regions they overwinter as small numbers of adults, or ephippia (resistant eggs). Populations increase roughly exponentially in the spring, chasing a rapidly growing algal population, to reach a peak of 20-100 animals per litre. Then, during the latter phase of this increase, both brood size and the proportion of reproductive adults decline, as the animals begin to make significant inroads into their food supply (George and Edwards, 1974; Hebert, 1978). The population may collapse shortly thereafter, and undergo one or more similar cycles later in the year (Fig. 7.7a, c) or alternatively (recall eq. 7.9) stabilize (Fig. 7.7b) until winter switches things off. This qualitative sequence of events is exactly that described by eqs. 7.5 and 7.6 when the system starts with  $V$  and  $H$  both small, and the plants ( $V$ ) are given a head start.

Inevitably there are complications. Sometimes, the *Daphnia* are dragged down by a decline in algal numbers, without contributing significantly to the crash through overgrazing. Instead, the algae exhaust essential nutrients ( $\text{SiO}_2$ , or P, for example), dramatically changing  $K$  (or  $r_1$ , depending upon your taste) in eq. 7.5 (e.g. Kilham, 1971, and references therein). Now, it is no longer true that plants cannot influence the supply of important resources available for the next generation (in the simple manner assumed on page 136), and plant growth must be modelled by choosing more complicated equations (e.g. Parker, 1968; Phillips, 1978).

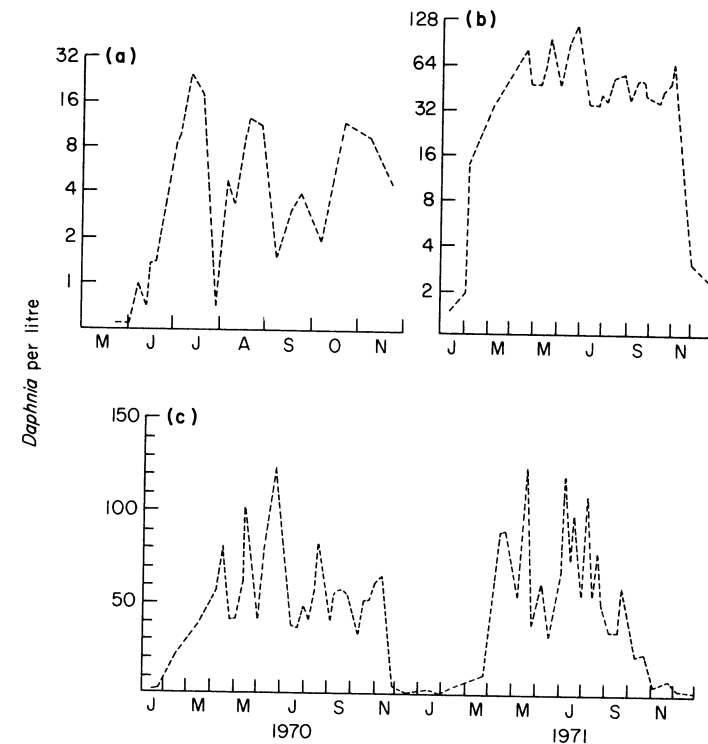


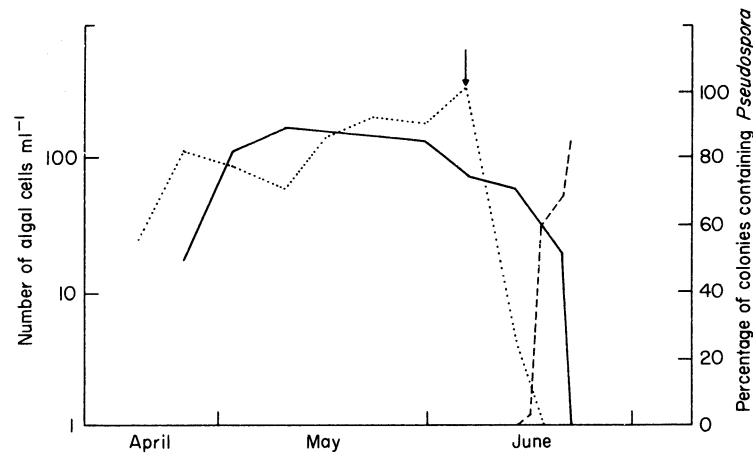
Fig. 7.7. *Daphnia* population dynamics in three different water-bodies. Growth in spring is approximately exponential until overgrazing limits further growth. The populations then fluctuate, or roughly stabilize around some average value until winter switches things off (George and Edwards, 1974; Hebert, 1978).

A second, planktonic example which certainly involves overgrazing is shown in Fig. 7.8.

#### 7.4.2 Interferential systems

When herbivores interfere with each other's grazing, the previous model is no longer appropriate. In contrast to the laissez-faire systems of section 7.4.1, the per capita rate of increase of herbivores is a function of both plant density and animal density.

From among the many qualitatively similar possible models (see, e.g., Table 5.1), we choose one which has already been discussed in section 5.2 (see Figs. 5.1 and 5.2), and has had detailed attention in



**Fig. 7.8.** Overgrazing of algal populations (*Gemmellicystis imperfecta*) by protozoa tentatively ascribed to the genus *Pseudospora* (Canter and Lund, 1968). The protozoa are grazing herbivores, with an amoeboid feeding stage, ingesting algal cells whole. Algal populations in the north (—) and south (· · · · ·) basin of Windermere decline rapidly as *Pseudospora* populations (---) build up in the north basin, and after the protozoa were first observed in the south basin (at the date indicated by an arrow).

the literature (May, 1975a; Tanner, 1975):

$$dV/dt = r_1 V(1 - V/K) - c_1 H[V/(V + D)] \quad (7.11)$$

$$dH/dt = r_2 H(1 - JH/V). \quad (7.12)$$

Here  $D$  is inversely proportional to grazing efficiency at low plant density (being the characteristic density of vegetation at which the herbivore functional response saturates), and  $J$  is a proportionality constant related to the number of plants needed to sustain a herbivore at equilibrium. The other symbols are as previously defined (note that  $r_1$  and  $r_2$  are to be identified with the earlier symbols  $r$  and  $s$  of chapter 5).

The zero isocline for the vegetation  $V$ , along which  $dV/dt = 0$  for any given  $H$ , follows from eq. (7.11):

$$H = (r_1/c_1) (1 - V/K) (V + D). \quad (7.13)$$

The zero isocline for  $H$ , along which  $dH/dt = 0$ , is similarly

$$H = V/J. \quad (7.14)$$

This latter isocline slopes out from the origin, in contrast to the vertical isocline of eq. (7.7). A further contrast lies in the stability properties of this model, which allow the possibility of a stable equilibrium point to either the left or the right of the hump in the  $V$  isocline, at  $V = (K - D)/2$ . The details of the stability properties, as a function of parameters such as  $K/D$  and  $r_1/r_2$ , are discussed in Fig. 5.2 and the accompanying text; for a fully detailed exposition, see May (1975a, Appendix I).

Our example is provided by the moth *Cactoblastis cactorum*, which was introduced into Australia in 1925 to control the prickly-pear cacti *Opuntia inermis* and *O. stricta*. Extensive stands of dense pear averaging about 500 plants per acre were virtually wiped out within two years of their colonization by *Cactoblastis* (Dodd, 1940). Dodd's account of the initial spread is worth reading, as are the subsequent reverberations in the ecological literature (see for example, Annecke and Moran, 1978, and references therein). The post-crash equilibrium was first interpreted as a game of hide and seek between *Opuntia* and *Cactoblastis* (Nicholson, 1947; Andrewartha and Birch, 1954) and then as a stable equilibrium maintained by grazing, reinforced by larval interference (Monro, 1967, 1975; Birch, 1971).

The eggs of *Cactoblastis* are not laid at random. Their dispersion is doubly contagious in that they are laid in egg-sticks of around 80 eggs each and the egg-sticks are themselves clumped (Monro, 1967). Hence during the summer some cactus plants receive many more eggs than would be expected by random chance, and others escape infestation completely. The contagious distribution of *Cactoblastis* eggs greatly influences the outcome of grazing by the larvae. Since a loading of above about 1.5 sticks per cactus ensures destruction of the plant, much of the larvae's resource is wasted (Monro, 1967).

Dodd (1940) and Monro (1967) present enough data to allow a stab at the values of four of the six parameters of eqs. (7.11) and (7.12). A clue to  $r_1$  is provided by Dodd's observation that *Opuntia* can increase from root stock to 250 tons per acre in two years. Assuming the root stock weighs one ton, the rate of increase is around  $r = 2.7$ . That will be an overestimate of  $r_1$  because the growth is entirely vegetative. Our guess for a maximum rate of increase depending partly on sexual reproduction is  $r_1 = 2$ . The value of  $K$  is taken from Dodd's remark that 5000 plants per acre is a fair estimate. Two rough estimates of  $r_2$  can be made. At the beginning of the experiment 2750 eggs were received from South America and hatched in the laboratory. The adults

produced 100,605 eggs:  $r_2 = 3.6$  per year [i.e.  $\ln(100,605/2750)$ ]. Dodd indicated that in the field *Cactoblastis* could erupt from 5000 larvae to 10,000,000 per acre in two years:  $r_2 = 3.8$  per year. For different reasons both figures are liable to underestimate  $r_2$  which is set at 4.  $J$  comes from Monro's measurements of the summer generation at his B1 and B2 sites:  $J = 2.23$  in units of cactus plants per egg-stick. Parameters  $c_1$  and  $D$  cannot be estimated. However,  $c_1$  should be large to reflect plants damaged and killed by the larvae as a by-product of their feeding. This structural damage contributes most to  $c_1$ , vastly outweighing the contribution of ingested plant tissue.  $D$  should be small to reflect the uncanny ability with which female moths search out food plants on which to lay eggs.

Three outcomes are demanded of a simulation of this system: *Opuntia* must crash within two years to square with Dodd's observations, it must stabilize at around 11 plants per acre to reflect the summer density at Monro's B sites, and the equilibrium must be highly stable. These requirements are met by setting  $c_1 = 6$  and  $D = 4$ . Figure 7.9 shows a simulation of *Cactoblastis* invading a stand of cactus. *Opuntia* density is expressed as plants per acre and *Cactoblastis* as egg-sticks per acre, the archaic 'acre' being retained to preserve uniformity with Dodd's round figures. *Opuntia* crashes in the required time to a highly stable equilibrium of 11 plants per acre carrying 5 egg-sticks.

This strategic model containing only six constants has produced a cactus crash looking much like the real thing. A tactical model would contain more detail, particularly on the survival of root stock after the crash which often allowed a temporary resurgence of the cactus; but it is unlikely to produce an outcome differing in kind from that provided by the simple interferential model. We can speculate cautiously that the model has described the major determining forces of the system, a conclusion reinforced by the result from the same data translated into laissez-faire parameters and fed through that model [eqs. (7.5), (7.6)]: without larval interference a spatially homogeneous system with these parameters is spectacularly unstable.

Interference amongst more advanced herbivores may involve much more than the highly contagious distribution of eggs, and the ensuing 'exploitation' competition seen in the *Opuntia*-*Cactoblastis* system, particularly when the herbivores have territories ('contest' competition). Now, each successful herbivore acquires for itself a large portion of the resources for its personal use ( $J$  in eq. (7.12) large). Something very

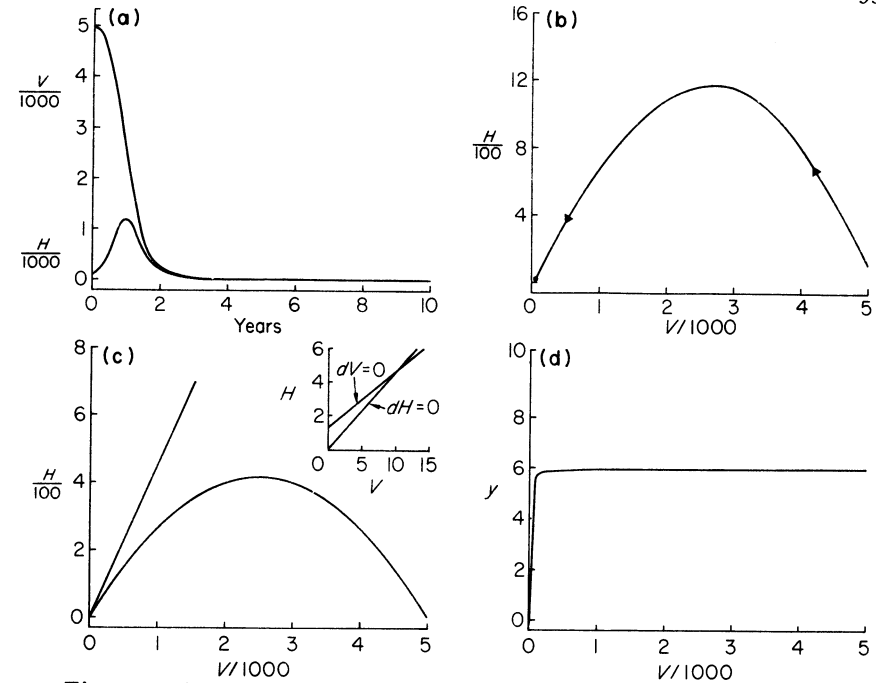


Fig. 7.9. The control of a plant by a herbivore. Graph (a) gives trajectories by the interferential model for a stand of cactus invaded by the moth *Cactoblastis*. Graph (b) shows the path to mutual equilibrium in phase space, graph (c) provides the modelled zero isoclines of cactus (curve) and *Cactoblastis* (line), and graph (d) is consumption per *Cactoblastis* egg-stick against cactus density.

like this apparently happens in an avian herbivore, the red grouse (*Lagopus lagopus scoticus*).

Shoots and flowers of heather (*Calluna vulgaris*, a small, woody, ericaceous shrub) make up at least 90 per cent of the diet of red grouse over most of the year, and heather is the dominant and sometimes virtually the only higher plant on the moors where grouse live. The population dynamics and nutrition of this unusual bird are described by Lance (1978), Miller and Watson (1978), Watson and Moss (1972) and references therein. The size of the breeding population is determined by the number of territories chosen by cocks in the previous autumn. Non-territorial birds are forced off the moor, suffering the brunt of the overwinter mortality, but will readily occupy territories if vacant lots are created by shooting. In other words, interference is very strong. As a result heather moors support rather a lot of heather and relatively few grouse, which eat somewhere between one and a half and two and a

half per cent of the total annual heather production (Savory, 1978). Quite why grouse have such large territories in relation to their apparent food supply is not clear, although the heather's nutrient content varies within and between areas, as well as with season, plant part, and plant age: 'heather' in other words does not necessarily equal 'food' (cf. hypothesis 1 on page 136). The grouse themselves are fastidious feeders on the most nutritious plants and plant parts, with patchy heather and heather of a high mean nitrogen content per shoot tip favouring smaller territories, and a higher density of birds (reducing  $J$  in eq. 7.12). Hence grouse populations respond to the availability and rate of production of their food supply, caricatured by eqs. (7.11) and (7.12.) The reciprocal impact of the grouse on the heather is much more difficult to judge, because as a woody perennial, with mixed sexual and vegetative reproduction, ill-defined individuals, and variable allocation of resources to roots, shoots and flowers under different grazing regimes (Harper, 1977), the plant is a paradigm of the problems confronting plant population dynamicists. Thus, although the birds probably eat less than three per cent of the total annual production of shoots and flowers, as much as twenty per cent of the suitable heather in the most heavily grazed age class might be consumed (Savory, 1978).

Obviously as a detailed model of the grouse-heather interaction, eqs. (7.11) and (7.12) are rather poor. In particular, eq. (7.12) cheats because it specifies nothing about the behaviour of the birds; instead, it simply defines its consequences in the term  $J/V$ . Models of exploiter-victim systems with explicit social hierarchies in the exploiter populations are developed by Gurney and Nisbet (1979). Comfortingly, and in keeping with the family of 'interference' models developed in chapter 6, their qualitative message is the same: behavioural interference is strongly stabilizing.

#### 7.4.3 *Interference or environmental heterogeneity?*

In most cases of clearly interactive systems we have no idea whether the herbivores interfere significantly with one another or not. If we move up a trophic level to chapter 6 we see strongly depressed host populations stabilized *either* by real behavioural interference between searching parasitoids *or* by spatial heterogeneity, the patchy distribution of hosts and the parasitoids' response to that distribution; and on balance the latter seems much more important than the former (Beddington *et al.*, 1978; Hassell, 1978). For plants and herbivores this

problem appears to translate itself into the difference between Nicholson, Andrewartha and Birch's hide-and-seek explanation for the *Opuntia-Cactoblastis* interaction, and the interference model outlined in the previous section. In practice, the difference is more apparent than real.

The ratio  $V^*/K = q$  provides a useful empirical measure of the impact of herbivores on plant populations, exactly analogous to  $q$  in predator-prey, or host-parasitoid interactions (Beddington *et al.*, 1978; chapter 6). Implicit in eq. (7.10) is the notion that strong, stable depression of the plant population ( $q \ll 0.5$ ) can be accounted for by behavioural interference between the herbivores, or by spatial heterogeneity. Neither complication needs be invoked to explain the stability of the interaction if  $q \gtrsim 0.5$ .

The *Opuntia-Cactoblastis* interaction is but one of several examples where  $q$  can be estimated or 'guesstimated' in cases of successful control of weeds by phytophagous insects. The plant populations are often spectacularly reduced (Clausen, 1978; DeBach and Schlinger, 1964; Harris, 1973). Estimates of  $q$  are provided in Table 7.3; see also Fig 6.9. Arguing largely by analogy from Chapter 6, it is not difficult to believe that spatial heterogeneity is just as important in the persistence of these plant-herbivore interactions as it is for strongly depressed insect hosts and their parasitoids; either in the form of hide-and-seek between attacker and attacked, or a safe physical refuge for the victim in a part of its environment. A refuge from the ravages of the beetle *Chrysolina* exists in woodland for St. John's wort (*Hypericum*), and a reserve of plant biomass unavailable to grazing mammals provides a powerful stabilizing influence in Noy-Meir's general analysis of systems with fixed herbivore numbers (Noy-Meir, 1975).

Intriguingly, 'interference' in the *Opuntia-Cactoblastis* system was a direct consequence of the aggregated distribution of eggs by the female moths, leaving a reserve of plants undiscovered and unscathed. An identical clumped distribution of attacks by insect parasitoids also manifests itself as apparent interference (Comins and Hassell, 1979; Free *et al.*, 1977; May, 1978a) and for exactly the same reasons. Exploitation competition is most intense in regions of strong exploiter aggregation. Examples of the non-random distribution of plants, and of the herbivores' responses to these distributions are touched upon in section 7.4.1. Figure 7.10 shows the aggregative response of an insect herbivore, the cinnabar moth (*Tyria jacobaeae*) to clumps of its food plant, ragwort (*Senecio jacobaeae*). At high densities, exploitation competition between caterpillars is intense (Table 7.2). Even when plants are spread



## 7.5 Extensions and elaborations

### 7.5.1 Extensions to more than two species

The notion that plant-herbivore interactions usually involve two species is obviously cheating, if not actually a downright lie; indeed if we are to peer deeper into the role of herbivory in plant communities, pretending that only two species are involved no longer works. Instead we must consider sets of plants and guilds of herbivores.

Guilds of phytophagous insects feeding in concert markedly influence the growth of individual hosts (Gradwell, 1974; Kulman, 1971; Morrow and La Marche, 1978), changing the demography and hence the dynamics of plant populations (Waloff and Richards, 1977; Fig. 7.11; see also Clements, Gibson, Henderson and Plumb, 1978; Connell, 1975; J. Foster, in Harper, 1977; Janzen, 1970; Perkins, 1978; Stephens, 1971). Other herbivores, fungal and viral pathogens often compound these effects. Whether the impact of herbivore guilds would be as dramatic in the absence of the majority of rare, apparently non-interactive species (section 7.3.2) is unknown.

Harper (1977) and Whittaker (1979) show convincingly how moderate levels of grazing have quite disproportionate effects on the population dynamics of plants by tipping the balance between competitors (see also Simmonds, 1933). In the simplest case (that of 'predator mediated coexistence') grazing reduces or eliminates competitive exclusion (Paine, 1966; see May, 1977c for a review); but depending upon such factors as the abundance of the exploiters, their feeding preferences, and on whether these are changed by encountering different frequencies of plants ('switching': see Rausher, 1978) the diversity of the vegetation may be enhanced or markedly reduced by grazing. Appropriate examples are provided by Connell (1975), Estes and Palmisano (1974), Harper (1977), Lubchenco (1978), McCauley and Briand (1979), Patrick (1975) and Porter (1973), for herbivores as varied as rabbits, voles, sea urchins, periwinkles, freshwater snails and zooplankton.

The most remarkable interpretation of the role of herbivory in altering the competitive balance between species of plants is that of Stanley (1973a), who invokes exploiter mediated coexistence to account for the major flowering of multicellular algae and most of the known phyla of multicellular animals near the beginning of the Cambrian.

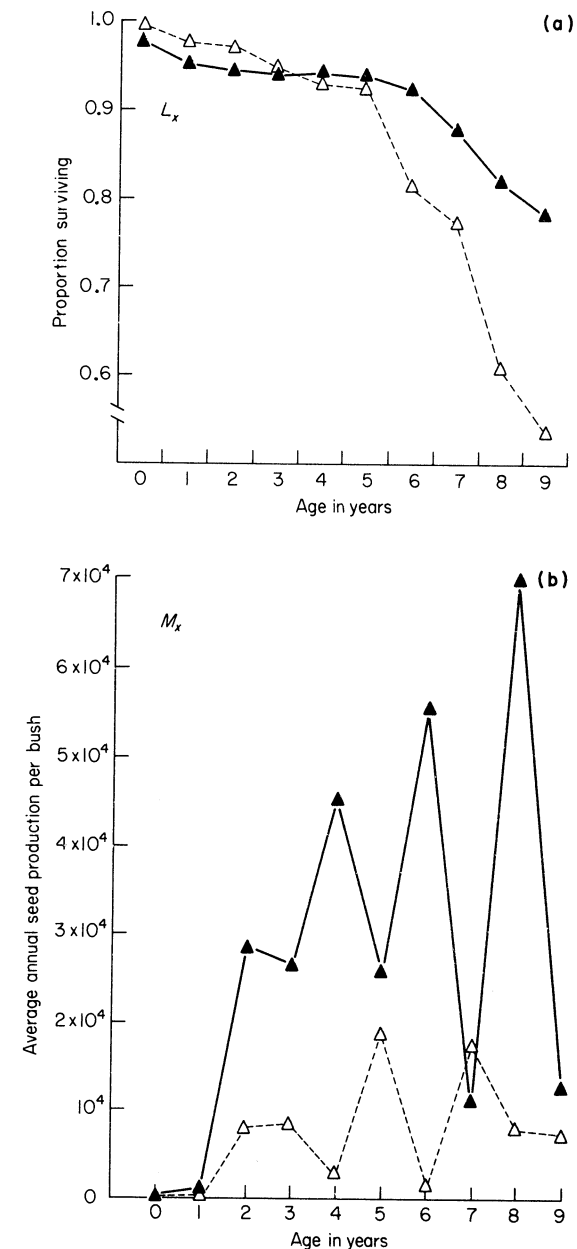


Fig. 7.11. The effect of removing herbivorous insects (by regular spraying with the insecticides demethoate and malathion) on survivorship ( $L_x$ ) and fecundity ( $m_x$ ) of broom bushes *Sarothamnus scoparius* (Waloff and Richards, 1977). Sprayed bushes ( $\blacktriangle$ ) apparently survive better and have higher fecundities than unsprayed bushes ( $\triangle$ ).

Certainly the late Precambrian leap in diversity is as remarkable as it was slow to start. Stanley argues for a Precambrian world with a relatively impoverished number of producers, bacteria and single-celled algae, limited by inter-specific competition for resources. When grazers finally evolved, perhaps 2.5 billion years after life first appeared on earth, the ensuing reduction in competition amongst the producers made possible the coexistence of many more sorts of plants, and released an orgy of evolution in both exploited and exploiter trophic levels. Under Stanley's hypothesis grazing transformed the world.

Whether a particular herbivore has, or has not, a significant impact on its food plant also depends upon the trophic stack extending above it. We have already argued the case for many phytophagous insects being kept rare by natural enemies. Many promising herbivores imported for biological weed control failed because of the impact of indigenous predators (Goeden and Louda, 1976). Similarly, sea otters will sometimes so deplete sea urchin populations as to change the whole appearance of the coast (Estes and Palmisano, 1974). On the western Aleutian Islands, the urchin-otter interaction involves four levels. On islands where man (level four) has eliminated otters (level three), sea urchins (at level two, and a favourite food of otters), thrive and kelp beds (level one) are eliminated by urchin-grazing. Without man, otters and kelp thrive, and urchins play 'pig in the middle'. The general implications of this game are intriguing (Fretwell, 1977) but largely ignored. Other things being equal, systems with an even number of trophic levels (2 and 4) are more likely to be interactive at the plant-herbivore level than are systems with an odd number of steps in the food chain.

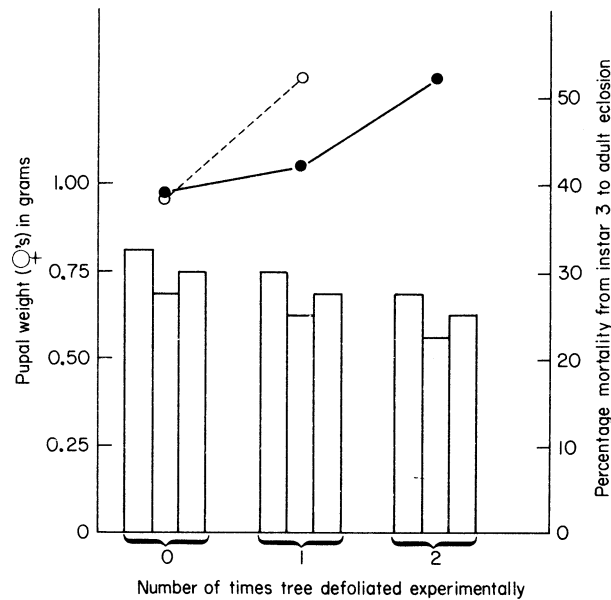
### 7.5.2 *Some evolutionary considerations*

The plethora of spines, irritating hairs, poisons and other protective devices evolved by plants bear strong witness to the selection pressures imposed by grazing. In consequence, most species of herbivores are unable or unwilling to eat most species of plants: herbivory is a trade for specialists, with adapted herbivores forced to attack only particular plants and parts of plants, often during a restricted season; or to feed and develop slowly and with high mortality on suboptimal diets (Lawton and McNeill, 1979). Such effects are sufficient on their own (hypothesis (1), page 136), or in combination with adverse climatic conditions and natural enemies (Lawton and McNeill, 1979) to keep most species of herbivorous insect (and presumably many other

herbivores as well) rare, most of the time. This deceptively peaceful stalemate reveals its true colours when man unwittingly breeds vulnerable varieties of crops (Day, 1972; van Emden and Way, 1973; Pathak, 1975) and when drought, other stresses, or even unusually favourable growing conditions so alter a plant's defensive chemistry as to create a major herbivore explosion (Newsome, 1969; White, 1969, 1974, 1976).

The evolutionary response of plants to grazing need not simply be in permanent defences. Animals when attacked by pathogens or parasites display a bewildering battery of induced defences (chapter 14); are there equivalent 'immune responses' to grazing in plants? For an individual algal cell swallowed whole by a *Daphnia* the question is obviously meaningless. But for trees and caterpillars, grass and voles it is not. Its importance rests, amongst other things, upon our ability to model plant-herbivore interactions successfully, because an 'immune response' turned on and off as grazing pressures rise and fall (an example of which was discussed in section 2.4.4) transforms the constants  $c_1$ ,  $c_2$  and  $d_2$  in eqs. (7.5) and (7.6) into variables; and if there are costs to the plant, alters  $r_1$  (and conceivably even  $K$ ) as well. As Haukioja and Hakala (1975) point out, such a reciprocal interaction between plant and herbivore gives an additional twist to, or provides a basic mechanism driving, herbivore cycles (section 2.4.4) and periodic outbreaks (see also Lomnicki, 1977, and references therein). Evidence for changes in plant-chemistry following grazing is provided by Haukioja and his co-workers (Haukioja and Hakala, 1975; Haukioja and Niemela, 1979); see also the discussion in section 2.4.4. Some, like the widespread production of wound induced proteinase inhibitors after localized tissue damage (Ryan and Green, 1974) play an enigmatic role in defence. The advantages of others, for example a marked reduction in the performance of caterpillars fed foliage from previously defoliated trees (Haukioja and Niemela, 1979; Thielges, 1968; Wallner and Walton, 1979; Fig. 7.12), are immediately apparent. We urgently need to know how quickly such responses decay, and whether any are permanent.

Plant defences, permanent or ephemeral, attest the obvious: being eaten is usually a bad thing. However, and unlike predation, grazing does not always or even often equal death, tempting both Harris (1973) and Owen and Wiegert (1976) to speculate that some grazing by insects may actually benefit the plant; see also the discussion in chapter 15. The chain of arguments in Owen and Wiegert's hypothesis is long, involving for example, secretion of copious quantities of honeydew



**Fig. 7.12.** Effects of experimentally defoliating grey birch trees, *Betula populifolia*, on the subsequent growth and survival of Gypsy moth, *Lymantria dispar*, with unrestricted access to leaves from control or treated trees (Wallner and Walton, 1979). Pupal weights (histograms) were significantly reduced in three populations reared on leaves from defoliated trees: the effect is more marked after two defoliations. Since fecundity in many Lepidoptera is proportional to female size, a herbivore outbreak leading to defoliation may reduce the rate of increase of subsequent generations of moths. Larval survival (solid and dotted graphs) is also worse on previously defoliated trees.

(excess sugars from the phloem sap) by aphids, with the honeydew then stimulating nitrogen fixation in the soil below the plant. Whatever benefits may in theory accrue to the plant through increased nitrogen availability (see Stenseth, 1978), they are not yet known to work in practice, because aphids impair rather than stimulate, the growth of trees (Dixon, 1971a, b; see also 7.3.2 and 7.5.1); at the moment, Owen and Wiegert's hypothesis has no experimental support.

More conventionally, compensatory growth upon being grazed is well established as a major adaptive component in the repertoire of many plants. McNaughton (1979a) provides a general review, and examines in detail the effects of heavy grazing by ungulates in the Serengeti. Here, moderate grazing stimulates productivity up to twice the levels in ungrazed control plots. Equation (7.5) implies plant productivity will be

maximized when  $V/K = 0.5$ , but McNaughton's review hints at far more than a passive response as plant biomass is depressed below  $K$ . With ungulate grazing  $r_1$  can no longer be viewed as a constant, but as a variable which will be increased, amongst other things, by: (1) increased photosynthetic rates in residual tissue; (2) reallocation of substrates from elsewhere in the plant; (3) mechanical removal of old, senescent tissue; (4) nutrient recycling from dung and urine; and last but not least (5) direct effects from growth-promoting substances in ruminant saliva (see also Dyer, 1980).

Finally, grazing may also drastically alter the partitioning of plant resources between roots, stems, flowers and leaves, and between sexual and vegetative reproduction (Harper, 1977; see also chapters 3 and 15); presumably many of these shifts in the resource budget are again adaptive. Thus defoliation may not only alter the growth rates and survival of trees (page 141) but also reduce their seed production (Rockwood, 1973). The herb *Solidago canadensis* responds to gall-forming insects by increasing stem growth and decreasing rhizome and seed production (Hartnett and Abrahamson, 1979); and the leek, *Allium porrum*, has a graded series of responses to attack by caterpillars of its own species of moth, *Acrolepiopsis assectella* (Boscher, 1979). Attack on one leaf stimulates axillary buds to flower; moderate levels of attack increase seed production; whilst heavy damage reduces seed production but increases bulblet formation (vegetative reproduction). The long-term consequences of these changes in resource allocation for the population dynamics of plants are largely unknown. But they are obviously extremely difficult to accommodate within the existing framework of Lotka-Volterra models.

### 7.5.3 Models

By now, it should be obvious that the art of modelling grazing systems, and hence our theoretical understanding, lags a long way behind the predator-prey and host-parasitoid interactions dealt with in chapter 6. The reasons are both sociological and biological: sociological because botanists have been peculiarly reluctant to study plant population dynamics, botanists and zoologists equally reluctant to abandon their training and straddle the first two trophic levels; and biological because the problems are not easy. Unlike 'prey', individual plants may be difficult, if not impossible to define; grazing rarely results in death, but can so alter the demography of the plant as to make it virtually a



different beast; and vegetative reproduction or buried seed banks all add to the confusion. In brief, realism resides in a jungle of parameters, most of them as yet unstudied and unmeasured except in the most rudimentary way.

For many systems, particularly when the herbivores are small and short lived relative to the vegetation, the most promising way forward appears to be to model plants as a 'population of parts' (see chapter 3), coupling the herbivores' dynamics to the bits which they eat. The idea has been most clearly developed, and the best data gathered by Gutierrez and his co-workers, particularly for cotton (see Gutierrez, Wang and Jones, 1979; Gutierrez, Wang and Regev, 1979; and Wang, Gutierrez, Oster and Daxl, 1977 and references therein). Their model views the plant as separate, but interacting, populations of leaves stems, roots and fruits, with submodels describing the dynamics of each. These submodels are integrated via a 'carbohydrate pool' which distributes available photosynthetic material, and provides the essential link between, for example, the amount of leaf tissue and subsequent fruit production.

Population models for the herbivores (e.g. pink bollworm, *Pectinophora gossypiella*, and Lygus bugs, *Lygus hesperus*) are coupled to the plants by making their birth, death, immigration and emigration rates functions of food availability and their own population densities. The herbivores alter the dynamics of plant parts in one or more of several different ways. For example, they may change the abundance and age structure of the leaves by eating them; if they are bugs, they directly reduce the carbohydrate pool; and if they attack fruits, they reduce seed production. Each of these effects, in turn, has consequences for the 'carbohydrate pool' of the plant and hence the dynamics of other plant parts.

The models are complex and have to be solved by simulation, but they can be applied to a wide range of plants and insects (Gutierrez, Wang and Jones, 1979). To date, the crop models describe very well what happens during a single growing season; they have not been used to simulate the dynamics of vegetation and herbivores over many generations. In all probability, such long-term simulations would require so many parameters as to be virtually incomprehensible without simplification. A similar problem has confronted, and been solved by, workers on spruce budworm *Choristoneura fumiferana* in the coniferous (*Abies* and *Picea*) forests of Canada (see Holling *et al.*, 1976; Peterman *et al.*, 1979 and references therein).

Budworms can increase rapidly in a matter of months: the trees in contrast take a decade to recover after an outbreak and have a life span of seventy years. Holling and his co-workers used their very complex simulation model to find the equilibrium points for insects and trees under various forest conditions. The resulting 'manifold' (Fig. 7.13b) distills the essence from an enormous amount of intricate biological detail. An immature forest supports only very low numbers of budworm, but as the forest matures, there comes a point where the budworm population is bound to explode. After a few years of outbreak densities,

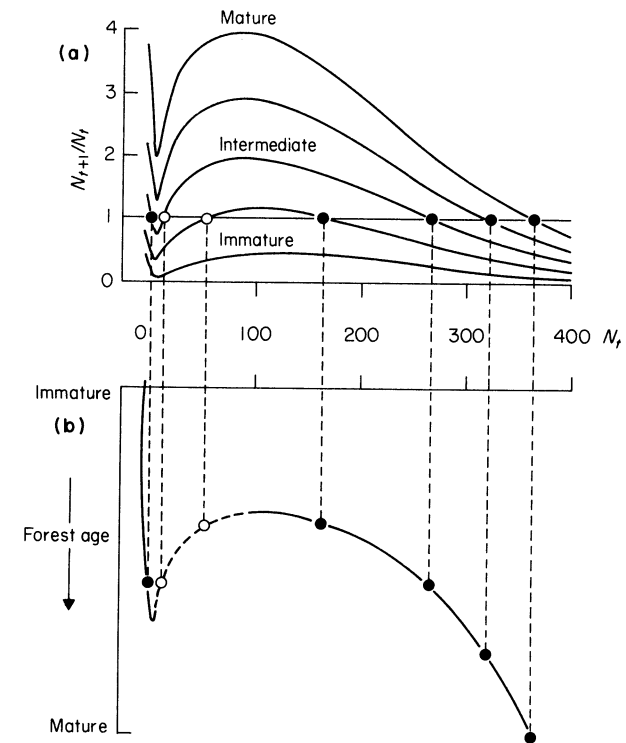


Fig. 7.13 (a). A family of budworm 'recruitment curves' for different levels of forest maturity. Plotted are points for each forest condition, where  $N_{t+1}$  and  $N_t$  are budworm numbers in two successive generations. (b) is a 'manifold' of equilibrium points, (where  $N_{t+1} = N_t$ ) and should be viewed sideways with forest maturity as the abscissa. Stable equilibria are represented by solid dots, unstable ones by open circles (Peterman *et al.*, 1979). The lower equilibria in young forests are apparently maintained by predation (hypothesis (3), p. 138): as the forest matures, predators become less effective and eventually the budworm 'outbreak' to the upper equilibria set by food limitation.

the old forest then deteriorates and is replaced, once more, by young trees. This example is discussed further in chapter 15.

Most plant-herbivore systems in which the herbivores are insects, and probably many vertebrate herbivore-plant interactions as well, share the 'nested hierarchy' of time scales characterized by cotton, spruce, and the beasts which eat them. Obviously, the births and deaths of caterpillars and leaves occur on time-scales orders of magnitude shorter than the births and deaths of trees. Such a nested hierarchy of time scales is identical to that seen in the dynamics of parasites and diseases of man and other vertebrates with indirect life cycles (May and Anderson, 1979; see also chapter 14). To model these interactions analytically, processes with the shortest time-scales are solved first, before being embedded in models of long-term events. Coupled with a detailed understanding of how the loss of one plant part affects the dynamics of other parts, we now have an exciting new framework within which to study plant-herbivore dynamics. At the moment such an approach to the dynamics of natural vegetation is no more than a glimmer in our collective mind's eye: we urgently need more data.

## 8

# Competition and Niche Theory

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### 8.1 Introduction: Definitions and Theoretical Background

#### 8.1.1 *Competition*

By definition, competition occurs when two or more organisms, or other organismic units such as populations, interfere with or inhibit one another. The organisms concerned typically use some common resource which is in short supply. Moreover, the presence of each organismic unit reduces the fitness and/or equilibrium population size of the other. Competition is sometimes quite direct, as in the case of interspecific territoriality, and is then termed *interference competition*. More indirect competition also occurs, such as that arising through the joint use of the same limited resources, which is termed *exploitation competition*. Because it is always advantageous for either party in a competitive interaction to avoid the other whenever possible, competition presumably promotes the use of different resources and hence generates ecological diversity. The mechanisms by which members of a community of organisms partition resources among themselves and reduce interspecific competition shapes community structure, and may often influence species diversity profoundly (see Schoener, 1974, for a review).

Ecologists are, however, divided in their attitudes concerning the probable importance of competition in structuring natural communities. Some, myself included, either tacitly or explicitly assume that self-replication in a finite environment must eventually lead to some competition. Other ecologists, particularly those that study small organisms and/or organisms at lower trophic levels, tend to be much more skeptical about the impact of competition upon organisms in nature. Still others have begrudgingly elevated competition to the status of a dogma—this school in turn emphasizes the importance of predation in structuring natural communities. While the persistence of