

Exploitation ecosystems in seasonal environments

Lauri Oksanen

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The model of exploitation ecosystems by Oksanen et al. contains a tacit assumption of constancy of the physical environment. Seasonality is a source of time delay in density dependent processes and thus potentially destabilizing. An analysis of grazing chain dynamics in seasonal environments where primary production is concentrated to a short and intense pulse (spring-summer or wet season) shows that the strength of this destabilizing force depends on reproductive potential and generation time. If annual reproductive output is low and juveniles are relatively vulnerable to moderate shortage of winter resources, then the model of Oksanen et al. applies to seasonal ecosystems, too. However, for rapidly reproducing herbivores with short generation times, seasonality is a strong destabilizing force. This destabilizing potential can be contained by generalist predators in environments where switching between small and medium-size prey is possible (temperate areas, continental taigas with soft snow), but should create sustained population fluctuations in environments with converse conditions (thick, hard and long-lasting snow cover). If the productivity of the area is low, the fluctuations should be chaotic and devastation of the vegetation should be the proximate cause of population declines in herbivores. In productive environments, the fluctuations should be regularly cyclic, and population declines of herbivores should be caused by the combined action of social regulation and predation. Available data conform to these predictions.

L. Oksanen, Dept of Ecological Botany, Univ. of Umeå, S-901 57 Umeå, Sweden.

The development of the hypothesis

Ecosystems seem to be orderly structured, and although chaotic dynamics sometimes occur (Schaffer 1985), a fair degree of constancy in abundance relationships between species seems to be the rule if radical external changes do not occur. Even birds, in spite of their small population sizes and exposed position in the top of a long food chain seem to retain fairly stable abundance relationships, changing only in response to changes in the environment (Järvinen and Väisänen 1978), and constancy of abundance relationships in the vegetation is the cornerstone of plant sociology and succession theory. Some ecologists are inclined to assume that this relative stability, indicating the existence of regulatory feed back loops, has not emerged by chance out of struggle for existence (Patten and Odum 1981, Odum and Biever 1984). However, already Hairston et al. (1960, referred to below as HSS) pointed out that order

may indeed emerge by chance from greedy exploitation: carnivores keep their resources – the herbivores – steadily overexploited and have guilds structured by resource competition. Due to the predation-limitation of herbivores, plants are relatively free from herbivory, so that also plant communities are structured by competition. The view of HSS on plant communities was quite traditional (Cajander 1909), and their ideas on carnivore/insectivore communities were not especially novel, either (Lack 1954). However, HSS put the different pieces together into a single, consistent hypothesis, which explained order without resorting to extra-Darwinian speculations.

The main criticism levelled against HSS referred to its realism: HSS had assumed that what is green is also potentially edible, which need not be the case (Murdoch 1966). However, evidence from systems grazed by a mixture of domesticated herbivores (cattle, horses, sheep and goats) supports the green-is-edible assump-

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tion of HSS, and similar evidence is also obtainable from natural systems without predators (see Oksanen 1988). But is the hypothesis also as general as claimed by HSS? This question became urgent for S. D. Fretwell when he was asked to create a theoretical backbone for a planned ecosystem project on a piece of Midwest (Konza) prairie. The scanty grass cover of hilltops did not amount to any apparent surplus of forage and the historical evidence was not sanguine to the idea that bison populations had been limited by predation (see also Sinclair 1977). Yet, the view of HSS seemed to be relevant for other habitats in the study area (slopes with tallgrasses, oak woodlots along creeks).

Fretwell's (1977) solution was to accept the general logics of HSS, but to assume that food chain length is constrained by primary productivity. HSS was proposed to apply to relatively productive ecosystems where food chain length is three links. In barren habitats, the grazing chain was supposed to consist of two links only, leaving grazers free from predation and able to regulate their food plants. The same logics were extended to extremely barren desert ecosystems, which were supposed to only have the first trophic link and to extremely productive marshes, supposed to harbor four link grazing chains. With this approach, Fretwell solved the problems that he faced on the Konza Prairie, but new problems immediately emerged. The idea of productivity and food chain length was taken from Odum's (1971) bottom-up approach to ecosystems and was thus an odd companion to the top-down view of HSS. Moreover, food chain length does not seem to vary in relation to primary productivity (Pimm and Lawton 1977, Pimm 1982), and it is difficult to translate the idea of marshes as four link ecosystems into names of organisms at these trophic levels (but see Fretwell 1987).

Fretwell was well aware of these problems. As a response to the criticism that he had blended two fundamentally different approaches, Fretwell proposed that the whole hypothesis must be reconstructed by means of standard exploitation models, with primary productivity as the independent variable. This was done by Oksanen et al. (1981). The core of Fretwell's (1977) proposition was found to be robust, although the lengthening of food chains to four links turned out to be just a possibility, not an inevitable consequence of enrichment. The model of Oksanen et al. (1981) also resolved large parts of the apparent conflict between Fretwell (1977) and Pimm (1982). Systems with two-link dynamics were found to easily have a locally unstable herbivore-plant equilibrium, generating periodic outbreaks during which predators can invade the area. Moreover, predators in the sense of exploitation models are only a subset of the third trophic level – those carnivores which are sufficiently efficient killers to subdue healthy adult prey. The presence of predators that are good at searching vulnerable prey but inefficient in killing healthy ones is thus compatible with two-link trophic dynamics and resource-limitation of herbivores (Oksanen and Ericson

1987a). The model also made one restriction of Fretwell's approach obvious. A relation between trophic dynamics and annual primary productivity of a habitat requires that the habitat is utilized in a fine-grained manner both in space and in time (i.e. consumers move between several plants and do it in all seasons). If this condition is not met, the original HSS hypothesis should apply even in barren ecosystems. Thus, the perspectives of Fretwell should only apply to vertebrates and to large, mobile arthropods with long life cycles.

Besides clarifying the logics and the limitations of Fretwell's (1977) ideas, the model of Oksanen et al. (1981) generated detailed predictions about the way how plant biomass should vary in relation to primary productivity. The IBP-data from arctic and subarctic areas are in good agreement with these predictions (Oksanen 1983). However, even for a proponent of Fretwell's approach, the model of Oksanen et al. (1981) can only be a little step towards understanding how ecosystems function. The model operates on large, homogenous areas, where movements of animals between different habitats do not occur, whereas real landscapes usually consist of a patchwork of habitats with large differences in primary productivity. The model does not include evolutionary responses to herbivory and predation, either. These restrictive assumptions have been relaxed by T. Oksanen (unpubl.) and L. Oksanen (unpubl.), but there were only a few situations (barren patches in areas where essentially more productive habitats abound, extremely nutrient-poor habitats) where the predictions of Oksanen et al. (1981) changed substantially.

The seasonality problem

Relaxation of the homogeneity assumption and inclusion of evolutionary aspects still leave one restrictive aspect of the model unchanged. Like all phase space models based on differential equations, the model of Oksanen et al. (1981) is based on the premise that all aspects of the physical environment which are relevant for the productivity of plants, herbivores and carnivores remain constant. For herbivores and carnivores, this condition is fairly well satisfied even in seasonal ecosystems. Even in the arctic, many small mammals reproduce throughout the year, if conditions are otherwise favourable (Fuller et al. 1977, Batzli et al. 1980). In large mammals, reproduction per se is pulsating, but the biomass and the consumption potential of a population is also dependent on the developmental stage of the animals. Thus, the effective density of grazer and carnivore populations increases gradually when juveniles grow and become weaned. However, a corresponding reasoning cannot be extended to the vegetation of a seasonal ecosystem. To make things worse, practically all gradients of decreasing primary production are also gradients of increasing seasonality. Thus, the seasonality problem goes to the core of Fretwell's reasoning,

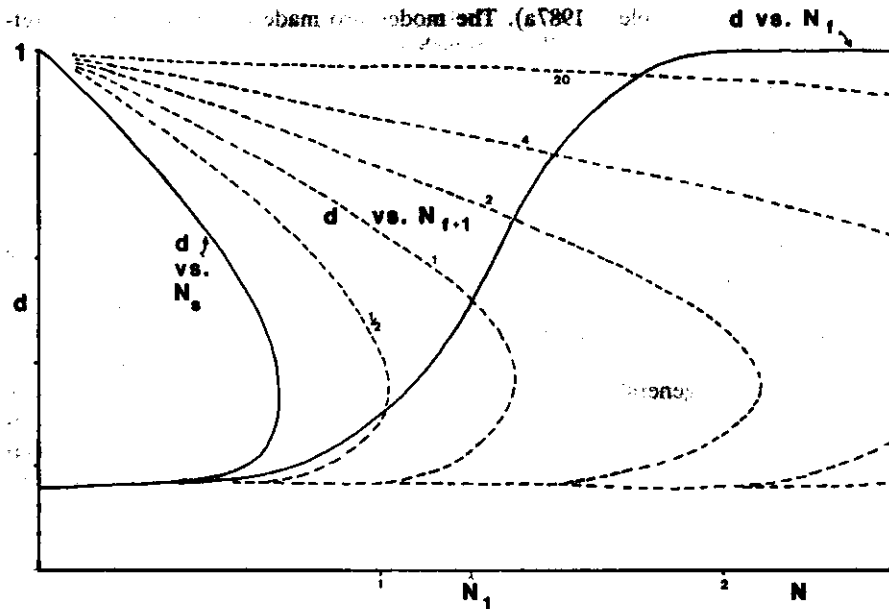


Fig. 1. Net winter mortality of herbivores (d) as a function of autumnal population density (N_t), and in relation to vernal population density (d vs N_t transformation) and to the population density in the subsequent autumn (d vs N_{t+1} transformation). The last-mentioned family of curves (dashed lines) has been drawn differently for herbivores with different reproductive potentials, from ungulate-type ($b = 0.5$) to microtine-type ($b = 20$) animals. The equilibrium autumnal density for $b = 1$ is marked by N_1 .

and it has been suggested that phenomena which seem to corroborate Fretwell's ideas are in fact consequences of increasing seasonality and their association with decreasing primary productivity is purely fortuitous (Hansson 1987).

Some results of Oksanen et al. (1981) seem applicable to seasonal ecosystems, as well. If the annual productivity is so low that herbivore populations are too sparse to be attractive to carnivores but are nevertheless dense enough to severely deplete the vegetation, carnivores will not be able to persist in the habitat, regardless of whether all primary production takes place in one day or is evenly distributed throughout the year. The resource-limitation of grazers in barren habitats thus seems to be a robust prediction, but day-to-day population dynamics are likely to be influenced. Exactly how destabilizing this form of resource renewal is and how it influences herbivore-resource dynamics is studied below.

Dynamics of seasonal herbivore-plant systems

To analyze the destabilizing impact of seasonality, it is useful to start with a system which is otherwise as free from destabilizing properties as possible. In standard consumer-resource models, lack of stability is a consequence of severe overexploitation of resources at equilibrium, creating a situation where temporary decreases in the density of consumers enhance the productivity of the resources (see Rosenzweig 1971, 1977). To exclude this possibility, I assume that the plant community completely recovers from grazing every spring, no matter how badly it was depleted in the winter. Although mainly aimed as a conservative assumption in analyzing destabilizing effects of seasonality, the assumption

seems fairly realistic for meadow and grassland ecosystems, exploited by non-fossorial grazers.

In such systems the dynamics of the vegetation become trivial. Thus we can focus on herbivores. Following Fretwell's (1972) models for populations in a seasonal environment, I define d as the net winter mortality of the population (number of winter deaths minus number of winter births, divided by the population size in the autumn, N_t), and b as its net summer natality (number of summer births minus number of summer deaths, divided by the vernal population size, N_s). For animals without winter reproduction, d varies between 0 and 1, but can obtain substantial negative values if winter reproduction occurs. The theoretical minimum value for b is -1 (all animals die in the summer), the maximum value depends on the reproductive potential of the species. At equilibrium, seasonal increases and decreases must balance, i.e. $(1 - d)(1 + b) = 1$ and $b = d/(1 - d)$.

To perform a stability analysis, we must find out how d behaves as a function of N_t and how b is related to N_s . For true herbivores, living on readily obtainable but depletable resources, the relation between d and N_t is easy to envision. When autumnal population densities are so low that resources will remain abundant throughout the winter, d will have some constant value which reflects the intrinsic mortality level for animals without winter reproduction and is negative if substantial winter reproduction occurs. If N_t is high enough to create acute food shortage well before the spring, d will be very close to one. In between these plateaux, there will be a steep rising portion, so that the $d(N_t)$ function as a whole is sigmoid (Fig. 1). To begin with, I assume that b is a species-specific constant, mainly for the sake of simplicity, but this assumption should also be rather realistic

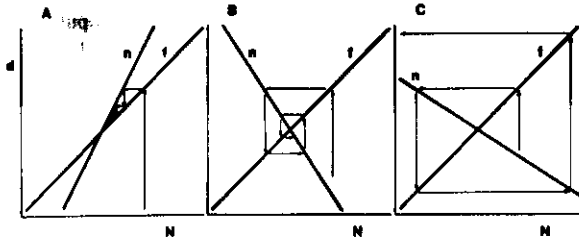


Fig. 2. A graphical neighbourhood stability analysis of a seasonal herbivore-resource system corresponding to Fig. 1. The $d(N_t)$ function is marked by f and the d vs N_{t+1} transformation curve by n . A: The transformation curve has a positive slope at equilibrium, thus it is stable and approached monotonously after perturbations. B: The slope of the transformation curve is negative but the transformation curve is steeper than the $d(N_t)$ curve. The equilibrium is stable and approached by means of dampening oscillations. C: The transformation curve has negative slope and is flatter than the $d(N_t)$ curve. The equilibrium now becomes a focus for diverging oscillations and is thus unstable.

in herbivore-grass systems, where summer resources are much more abundant than winter resources.

With the $d(N_t)$ function described, we can proceed to look at conditions for a stable equilibrium. An illustrative way for doing this is to use a modification of Fretwell's (1972) transformation curve technique. Let us define the first transformation of the mortality function as the relation between net winter mortality and the number of survivors in the next spring (d vs N_t transformation). This can be obtained by multiplying the abscissa of the $d(N_t)$ curve by $1 - d$. We then proceed to define the second transformation of the $d(N_t)$ function as the relation between net winter mortality and the population size in the next autumn (d vs N_{t+1} transformation, obtained by multiplying the abscissa of the first transformation curve by $1 + b$, see Fig. 1). We already know that the equilibrium (N_t^*) is in the intersection between the $d(N_t)$ curve and the second transformation (d vs N_{t+1}), because exactly that point satisfies the condition $(d - 1)(b + 1) = 1$. Choosing a value of N_t slightly different from N_t^* , we can see whether the equilibrium is locally stable. The appropriate winter mortality can be read from the corresponding point of the $d(N_t)$ curve, the population size in the next autumn can be read by moving horizontally to the second (d vs N_{t+1}) transformation curve, the net mortality in the subsequent winter by moving vertically to the $d(N_t)$ curve, and so on.

The essence of this procedure can be best captured by magnifying the neighbourhood of the equilibrium, so that the $d(N_t)$ curve and the d vs N_{t+1} transformation curve can be represented by straight lines (Fig. 2; this is equivalent to the standard analytical linearization technique). We immediately see that the stability of the equilibrium depends on the slopes of the two curves. If both curves have positive slopes, the equilibrium is stable and approached monotonously (2A). If the slope of the d vs N_{t+1} transformation curve is negative, but the

curve is steeper than the $d(N_t)$ curve, the equilibrium is stable and approached by means of dampening oscillations (2B). If the slope of the d vs N_{t+1} transformation curve is negative and its absolute value is smaller than the slope of the $d(N_t)$ curve, the system overcompensates, so that perturbations are followed by diverging oscillations (2C). Thus, the equilibrium is locally unstable.

Looking back at Fig. 1, we see that the stability of the equilibrium is critically dependent on net summer reproduction (b). The same $d(N_t)$ curve which yields a stable equilibrium for animals with $b = 0.5$ (a value typical for ungulates) creates an unstable equilibrium for $b > 5$ which is a typical situation for microtine rodents and also for many lagomorphs. This does not necessarily mean that resource-limited ungulates of seasonal environments always have stable populations and resource-limited small mammals always have unstable ones. As noted before, multiannual effects of foraging can easily destabilize any grazer population, provided that the habitat is not extremely barren (see Klein 1968, Oksanen et al. 1981). Conversely, social interactions can stabilize populations by making b density-dependent which makes the d vs N_{t+1} transformation curve steeper in the neighbourhood of the equilibrium (see also Łomnicki 1978, Stenseth 1986). The same effect can also be obtained, if b is highly sensitive to availability of rare high-quality food items (Hansson 1987). However, stabilization by territoriality is difficult to achieve, because of the difficulties in making forage a defensible resource. Pikas (*Ochotona* spp.) have managed to do this by harvesting the food (Broadbrooks 1965, Orr 1977, Southwick et al. 1986, Huntly et al. 1987), but their technique can only be successful in areas with dry summers and much sunshine. Hansson's hypothesis on dependence of summer reproduction on rare high-quality food items was, in turn, developed for the relatively granivorous bank vole and can hardly be applied to genuine folivores.

Numerical simulations suggest that seasonal herbivore-plant systems with a locally unstable equilibrium generate chaotic fluctuations, not cycles (Fig. 3), whether or not there are multiannual effects upon resource production and whether the herbivores have winter reproduction or not. This is easy to understand in the light of the results of May and Oster (1976). They found that the combination of discrete population growth and high reproductive potential generates a chaos even with linear density dependence. My assumption of density-independent b generates similar potential for overshooting as discrete population growth does, and the sigmoid $d(N_t)$ function is a further destabilizing factor, because it implies unlimited growth up to a critical population density, after which winter mortality rapidly becomes catastrophically high. Thus, heights of successive population peaks can differ by a power of ten, causing correspondingly different deepness of crashes and durations of low phases; for populations

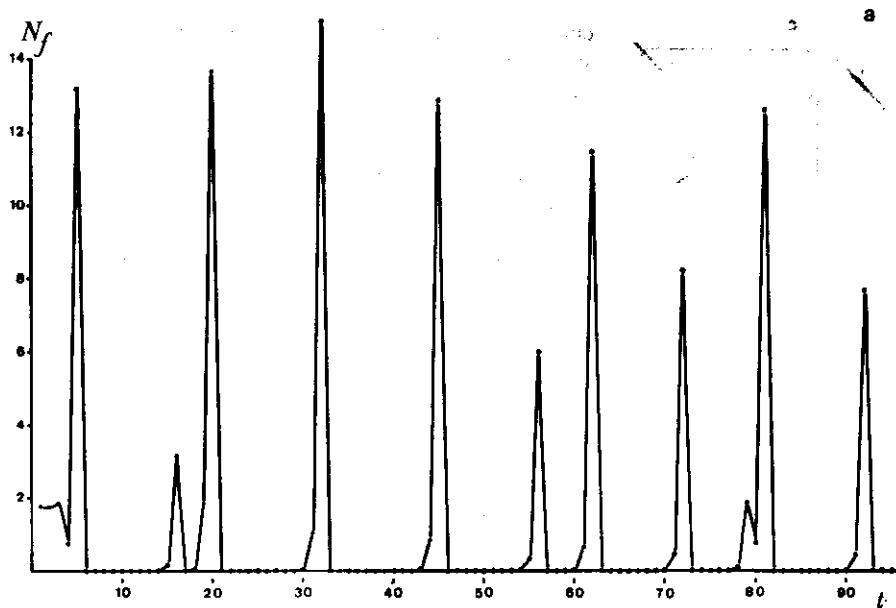
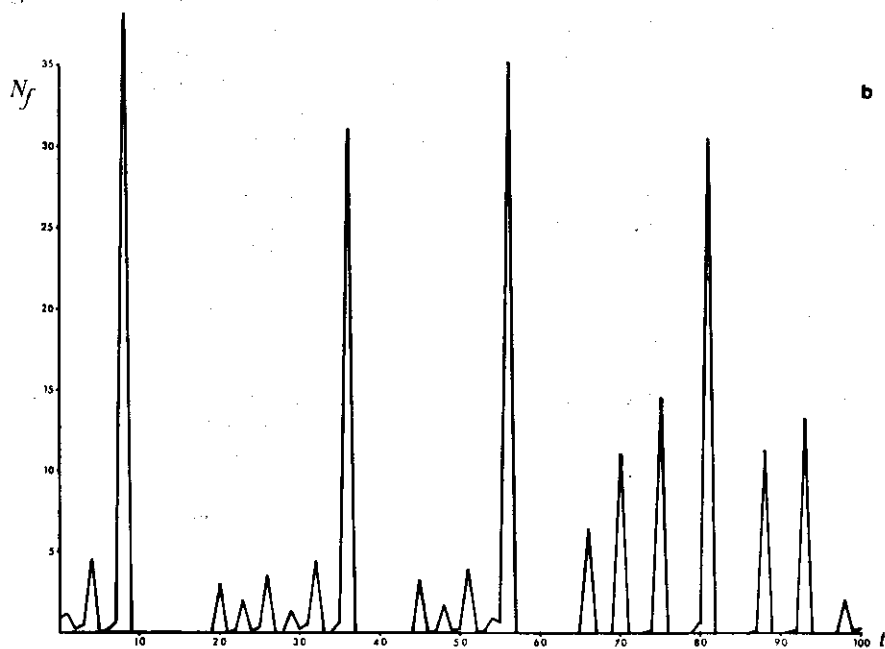


Fig. 3. Autumnal population densities in a simulation based on Fig. 1 (3a) and on a corresponding mortality curve with winter reproduction (3b). In these simulations, multiannual effects of resource depletion have been assumed. (After a catastrophic crash, winter mortalities were assumed to remain high during two subsequent years); runs without multiannual effects gave very similar patterns.



with winter reproduction, also peaks which build up from low levels during the winter and crash before the spring are possible.

Three link exploitation in seasonal environments

Whether the three-dimensional exploitation model of Oksanen et al. (1981) can be directly applied to dynamics of seasonal carnivore-herbivore-plant systems is a question of time scales. The salient feature that distinguishes three-dimensional (carnivore-herbivore-

plant) models from two-dimensional (carnivore-herbivore) ones is that the three-dimensional ones contain an additional stabilizing factor: the impact of forage depletion on the population growth of herbivores (Rosenzweig 1973, Wollkind 1976). For herbivores that must survive at least one winter as relatively vulnerable juveniles, seasonality does not remove this stabilizing factor. If, however, fully grown individuals can be produced during the summer, then depletion of winter resources will not be a source of gradual density dependence. We then have a situation where resources either remain sufficiently abundant for good summer reproduction

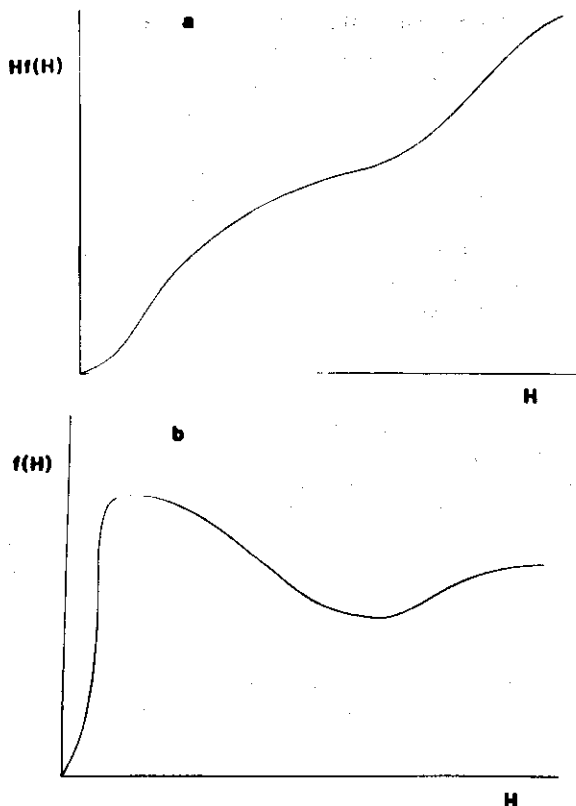


Fig. 4. Functional response ($H(f(H))$, 4a) and attack rate ($f(H)$, 4b) of an optimally foraging small specialist predator according to Abrams (1982) and Oksanen et al. (1985), in relation to prey density (H).

and high winter survival, or resources still allow good summer reproduction but run out sometimes during the winter, with catastrophic mortality as the most likely consequence (see previous section), so that any predator population dependent on this prey would be doomed.

The persistence of predators in seasonal systems with rapidly reproducing herbivores thus depends on their ability to prevent prey densities from reaching the critical level where resource depletion would cause catastrophic winter mortality. What properties the consumers should have in order to satisfy this condition and how the dynamics of a seasonal three-link system with rapidly reproducing herbivores should be studied by means of two-dimensional predator-prey models, subjected to the boundary condition that herbivore densities must not exceed a threshold set by the production of winter resources.

Recall that the prey population growth in a two-dimensional exploitation model is governed by

$$dH/dt = rH(g(H)) - f(H)HC \quad (1)$$

where H is herbivore density, r is the intrinsic growth

rate of herbivores, $g(H)$ represents density dependency of herbivore population growth, C is carnivore density and $f(H)$ is the risk that a given carnivore poses for a given herbivore in a time unit (to be called attack rate, see Holt 1977). The prey isocline can be obtained by setting $dH/dt = 0$ and solving for C which gives

$$C = r(g(H))/f(H) \quad (2)$$

Thus, what determines the course of the prey isocline is the ratio of per capita prey reproduction to attack rate (or the ratio of total prey reproduction, $Hr(g(H))$ to the functional response of predators, $H(f(H))$; the two statements are equivalent).

If the attack rate at equilibrium is an increasing function of prey density (i.e. if the functional response is stabilizing), the prey isocline will have a negative slope at equilibrium, guaranteeing its stability, as already shown by Rosenzweig and MacArthur (1963, see also Murdoch and Oaten 1975, Tanner 1975). Such stabilizing functional response is likely for predators with alternative resources, provided that the predator - alternative resource system has a stable equilibrium. A concrete example of how such a system could be formed has been documented by Erlinge et al. (1983, 1984). In the South Swedish old field ecosystem studied by this team, the dominating carnivores are generalists, capable of handling a wide range of prey sizes. Herbivores, in turn, form a continuous size distribution (field voles - water voles - rabbits - hares - roe deer). Thus, the rapidly and slowly reproducing parts of the grazer guild are linked by shared predators which can - and do - swiftly react to any increases in microtine densities.

As pointed out by Hansson (1979, 1987, 1985), the deep and relatively tightly packed snow cover which characterizes the oceanic sectors of the boreal zone effectively isolates wintering microtines from medium-sized predators. Thus, the relevant system for oceanic taiga areas consists of microtines and specialists capable of hunting in the subnival environment (e.g. weasels). For such a system, the high degree of specialization precludes significant switching. The main remaining factor that could lead to a positive relation between attack rate and prey density is the changing reward-risk balance of predation. Abrams (1982) showed that sufficiently low prey densities favour inactivity over desperate predation. Consequently, when prey density is in the neighbourhood of the level at which the cost-gain balance of predation becomes positive, strongly increasing attack rate is plausible even for strict specialists. Another range of prey densities where the attack rate of the predator can be an increasing function of prey density is when a substantial fraction of the prey density is excluded from shelters, due to intra- and interspecific competition. Surplus killing then becomes very cheap and can be committed because of absence of significant selection against such behavior (Kruuk 1972). If the killed prey are cached in dry or cold places, so that at

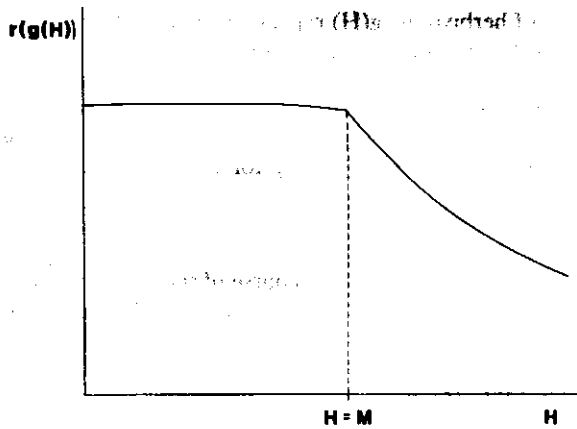


Fig. 5. Per capita population growth rate $r(g(H))$ of herbivorous small mammals as a function of population density, according to Stenseth 1986.

least a fraction of their food value is retained, natural selection can directly favour surplus killing, especially if the predators are unable to preserve live prey by means of territorial defense (Oksanen et al. 1985). Thus, as proposed by Abrams (1982), a plausible form of a functional response curve for a specialist has little to do with Holling's (1965) typology and is likely to have at least two stabilizing (downward convex) sections (Fig. 4a), which create corresponding humps in the attack rate curve (Fig. 4b).

There is much controversy about the existence of direct density-dependence due to agonistic behavior in herbivores in general and particularly in herbivorous small mammals (see Krebs 1978, Myllymäki 1977). At least in some species of herbivorous small mammals, female territoriality seems to exist and work as a 'social fence' (Hestbeck 1982, Stenseth 1986), both within and between species (Viitala 1977, Henttonen and Hansson 1984). When population densities are low or moderate, females have unlimited possibilities to establish territories, and per capita reproduction remains constant. At some threshold density, the 'social fence' closes, i.e. there is no space for further female territories. Those females which have managed to get a territory keep reproducing, but the remaining ones do not mature. Consequently, the average per capita reproductive output starts declining. The math is quite simple. Let M be the maximum number of female territories that can be established. Then, $g(H) = \min(1, M/H)$. Thus, $r(g(H)) = \min(r, rM/H)$. This is presented graphically in Fig. 5.

The general shapes of $f(H)$ and $r(g(H))$ functions give most of the information needed for constructing the prey isocline. What remains to be determined is how the coordinates of the two functions match (i.e. where M lies on the $f(H)$ curve). This has actually already been done. Closing of the social fence implies that the prey population starts producing floaters which move around searching for a vacant territory, and thus being exposed

to predators. Thus, the last increasing section of the attack rate curve should start at $H = M$. We can thus match the $f(H)$ and $r(g(H))$ curves and do the division. The resulting prey isocline is depicted in Fig. 6.

Construction of a complete carnivore-herbivore graph also requires knowledge of carnivores. Erlinge's (1974) study on least weasels suggests that also their female-female relationships work as a social fence. However, female territories turned out to be very small in relation to reported weasel densities. Thus, the social fence of weasels seems to remain open at realistic population densities, implying vertical predator isocline (Rosenzweig 1977). We also know that the predator isocline cannot meet the prey isocline at its leftmost section with a negative slope. This section represents prey densities so low that predation barely pays back the costs of activity, whereas at the predator isocline, the gains of predation must pay the costs of both activity and maintenance and also allow enough reproduction to balance mortality. The possibility that the predator isocline meets the prey isocline in the second portion with a negative slope (i.e. where the social fence of the prey is closed) cannot be denied out of hand. In fact, Henttonen (1987) suggested that this is the case for some agile and largely arboreal *Clethrionomys* species. However, at least for the more clumsy and ground-dwelling genuinely folivorous small mammals the only plausible place for the predator isocline is in the rising section of the prey isocline (Fig. 6). Consequently, systems dominated by such herbivores will generate sustained population cycles provided that the habitat is productive enough, so that the maxima of the cycles remain below the threshold for catastrophic winter mortality.

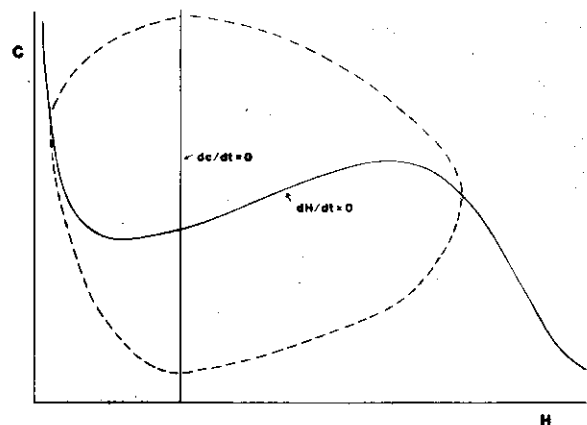


Fig. 6. Isoclines for a predator (C) - prey (H) system where $f(H)$ and $r(g(H))$ functions conform to Figs 4 and 5, respectively, and where predators are rather efficient in catching prey and strictly food-limited, without significant social regulation. The equilibrium is locally unstable and generates a stable limit cycle (dashed line) where social behavior has a central role in containing the population within the carrying capacity of the habitat and predation acts as the chief proximate cause of population declines (see Henttonen et al. 1987).

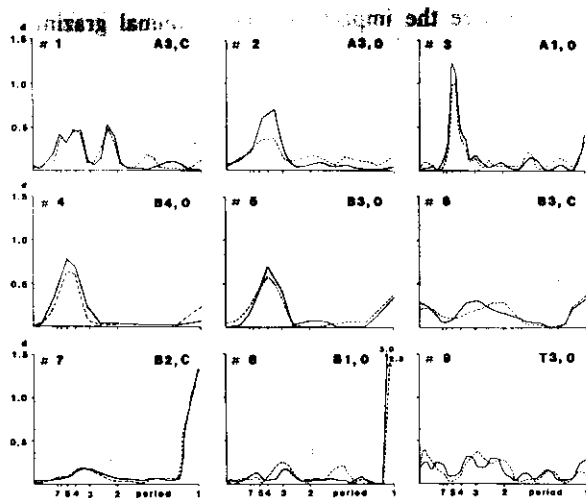


Fig. 7. Spectral density profiles, based on population records of small mammal studies with minimum duration of 14 yr and minimum trapping frequency (live or snap trapping) twice a year, using both raw (dashed lines) and log transformed (unbroken lines) data. In records where the trapping frequency was higher than twice a year, seasonal minima and maxima were used. The position of the study areas has been denoted by the zone/sector system of Ahti et al. (1968), with four major extratropical zones (A = arctic, B = boreal, T = temperate, M = meridional), each divided into four subzones (4 = northern, 3 = central, 2 = southern, 1 = transitional) and to oceanic (O) and continental (C) sectors. Periods are given in years. Sources # 1: Pitelka et al. 1973, Batzli et al. 1980, # 2: Framstad et al. 1988, # 3: Laine and Henttonen 1983, # 4: Henttonen et al. 1987, # 5: Hörnfeldt 1984, # 6: Mihok and Fuller 1981, # 7: Koshkina and Korotkov 1975, # 8: Ivanter 1981, # 9: Southern 1979.

Relation to grazing chain dynamics in real ecosystems

The above considerations imply that, regardless of seasonality, large grazers have generally stable populations – resource-limited and exerting strong herbivory in barren ecosystems (high- and middle arctic tundras and corresponding alpine belts, steppes and semideserts) and predation-limited in productive ones (forests, productive scrublands and meadows, tall grass plains, savannas). Ungulate-vegetation cycles are possible in transitional areas, and should be observed on islands without key predators. Until quite recently, the general idea has been that ungulates are resource-limited everywhere (Caughley 1976, Caughley and Lawton 1981, Sinclair 1977). However, the case has largely been built up on the basis of data from arid and alpine ecosystems (and could be supported by arctic data, see Thomas and Edmonds 1983, Tyler 1987). The case of moose on Isle Royale also seems to support the idea of resource-limitation, although this system is apparently characterized by a moose-browse cycle, with predators playing at least a minor role (Peterson et al. 1984, Peterson and Page 1988). However, Isle Royale is devoid of a key predator – the bear. In the presence of both wolves and bears, boreal populations of moose seem to be regulated by predation (Messier and Crete 1984, 1985). Sin-

clair's (1985) recent paper, in turn, amounts to a profound re-evaluation of the role of predators in ungulate dynamics of East African savannas. Although the debate is by no means settled, the idea of predator limitation of ungulates in relatively productive ecosystems is thus gaining ground.

In the case of small mammals, most studies reporting heavy devastation of the vegetation have been performed on typical arctic tundra or its altitudinal counterpart on boreal mountains (Tihomirov 1959, Kalela 1971, Batzli et al. 1980, Černjanskij and Tkačev 1982), whereas studies performed in the most luxuriant low arctic habitats (Krebs 1964, Oksanen and Oksanen 1981), in birch brushwoods (Tast and Kalela 1971, Laine and Henttonen 1983) and in the northernmost taiga (Henttonen et al. 1987) have failed to demonstrate corresponding massive devastation of the vegetation, although grazing impacts are observable and influence survival patterns of woody plants all the way down to the middle subzone of the taiga (Ericson 1977, Hansson 1988). The issue of predation limitation of herbivorous small mammals is, if possible, even more controversial than the idea of predation-limited ungulate populations. However, the strongest case for the idea that generalist predators prevent cycles from occurring is made by Erlinge et al. (1983, 1984, Erlinge 1987) who performed their study in a productive old field ecosystem in southernmost Sweden, and the best indications for predation as a proximate cause of decline in a microtine cycle come from a productive subalpine meadow area (Fitzgerald 1977), from a luxuriant birch brushwood habitat (Viitala 1977) and from moist taiga (Henttonen et al. 1987) which conforms to the implications of my reasoning.

A detailed review of long and medium term records of small mammal population dynamics is a matter of writing a book. However, a spectral analysis of the longest available records of small mammal populations which have been continuously trapped at least twice a year by methods that give reasonable density indices (snap trapping or live trapping) suffices to show the general pattern (Fig. 7). No sustained cyclic fluctuations can be demonstrated from temperate or continental boreal ecosystems i.e. from areas where snow is either largely absent or remains soft and thus gives little protection against medium-sized predators. Conversely, all long-term records from oceanic sectors of hemiarctic, north boreal and middle boreal zones (sensu Ahti et al. 1968) show regular multiannual cycles. The cyclic records represented in Fig. 7 all come from Fennoscandia, but this is probably a matter of differences in geography and funding policy between Europe and North America. In North America, oceanic taiga climate only occurs on the westernmost mountains (Tuhkanen 1985). This area seems to harbor cyclic *Microtus* populations, although even the best record (Fitzgerald 1977) is too short and discontinuous to allow definite conclusions. The largest part of boreal North America has a climate which does not occur in the Old World at all – with

continental thermal conditions but nevertheless enough moisture to create a thick snow cover. These conditions, requiring that animals must either be light enough for snowshoeing or big enough for wading in deep snow, have created a gap between the lynx-hare subsystem and the wolf/bear-ungulate subsystem. (Canadian lynxes and hares are less than half the weight of their North European counterparts, see Burt and Grossenheider 1968, Siivonen 1975.) Consequently, cycles are found in Canadian snowshoe hares (Finerty 1980), and at least some researchers regard predation by lynxes as an essential part of the cycle (Keith 1974, but see Bryant et al. 1983), and with microtines in the role of an alternative prey, tuned to the lynx-hare cycle (Mihok and Fuller 1981).

The records of lemming densities from graminoid-dominated middle arctic tundra habitats at Barrow, Alaska, and of lemmings and root voles from corresponding oroarctic (alpine) habitats at Finse, Norway, show by far the most violent density fluctuations in the entire material. Unlike the records from the Fennoscandian taiga, however, the spectral analysis fails to demonstrate the occurrence of regular cycles. The lemmings at Barrow (# 1 in Fig. 7) seem to have entirely chaotic density fluctuations. The Finse data set (# 2 in Fig. 7) is more complicated: the run based on raw data (dashed line) does not indicate any periodicity, whereas a clear spectral peak can be seen in the run based on log transformed data (unbroken line). This discrepancy is a consequence of fixed periodicity, combined with tremendous variation in the heights of population peaks which indicates intrinsically chaotic dynamics with externally imposed periodicity due to periodic immigrations from near-by areas with a genuine cycle. Other available records suggest that the cases of Barrow and Finse are representative for middle arctic tundras and their latitudinal counterparts on the Scandinavian mountains, respectively. In spite of their shortness, the records of density variation in arctic lemmings of Truelove Lowland, Devon Island, Canada (Fuller et al. 1977) and of Ostrov Vrangeli, Siberia, USSR (Černjavskij and Tkačev 1982) suffice to show that the populations fluctuate violently and in a way which is incompatible with the occurrence of regular, multiannual cycles. Medium-term records (duration of the study about 10 yr) from tundra habitats of northern Fennoscandia (Henttonen et al. 1977, Andersson and Jonasson 1986, Oksanen and Ericson 1987b) suggest that tundra and taiga/brushwood populations peak synchronously (compare with Laine and Henttonen 1983 and Henttonen et al. 1987), but heights of the peaks are much more variable on the tundra. The border between cycles and chaos seems to go between low arctic willow zone (e.g. the study area of Krebs 1964) and more extreme arctic-alpine grass and lichen-moss tundras. This borderline also seems to separate areas where profound and recurrent habitat devastation by small mammals has been reported from

areas where the impact of small mammal grazing is moderate or weak.

The data discussed above do not prove that the exploitation approach is a reasonable way to look at ecosystems and even if it were so, one can disagree about the merits of the specific ideas of Fretwell (1977) and Oksanen et al. (1981) and regard e.g. the views of Menge and Sutherland (1976, 1987) as having a wider range of applicability. The proposition of Fretwell and Oksanen et al. that predators are essential in controlling herbivore populations of productive habitats is just as controversial as the underlying HSS hypothesis which is currently intensely debated (Connell 1983, Schoener 1983, 1985, Sih et al. 1986). There is also a profound conflict between the traditional ecophysiological approach to geographical plant ecology (e.g., Walter 1966, 1968, Ellenberg 1978) and the view of Fretwell (1977) and Oksanen et al. (1981, see also Oksanen 1988, 1989) that typical tundra and steppe vegetation is a product of herbivore-plant interaction and would change beyond recognition in the absence of herbivores. Carefully designed field experiments will be needed for settling these issues. However, for those who regard Fretwell's approach as a promising one, the current inclusion of seasonality should be a welcome increase of realism. Its predictions on cyclic and chaotic population fluctuations are corroborated, whereas the corresponding predictions of Oksanen et al. (1981) are clearly in conflict with available data. Notice that the spectral analysis really is a test of previously deduced predictions. The first version of the current model (Oksanen 1981, developed in 1979-80) is older than most data sets in Fig. 7, and I was originally quite disturbed about the chaos prediction which was in conflict with the 'fact' (Pitelka 1973) that lemmings at Barrow are cyclic.

Although the inclusion of seasonality seems to be a step towards greater realism, it also amounts to a reduction of simplicity and elegance. Fretwell's original idea that trophic levels behave as homogeneous blocks creates beautiful graphs (Oksanen et al. 1981), whereas the look at life history characteristics of individual organisms is rather pedestrian. But this is biology and it is not reasonable to expect that simple models could in a complete and realistic way represent dynamics of biological systems. Models are just answers to specific questions - in the case of Oksanen et al., to the question whether Fretwell's (1977) verbal reasoning was logically consistent. Even if the reader were inclined to regard the model as a fair representation of principal differences between grazing chain dynamics in ecosystems with different primary productivity, it is still necessary to accept that a higher degree of resolution is needed when answering questions about day-to-day population dynamics.

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