

Exploitation ecosystems in heterogeneous habitat complexes II: impact of small-scale heterogeneity on predator–prey dynamics

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Summary

The model of exploitation ecosystems was re-analysed, assuming that habitat patches are so small that they form only parts of the home range of an individual predator. For habitat complexes where productive patches abound, the results suggested that predation will strongly spill over from productive patches, which set the tune for population dynamics within the whole landscape, to barren ones. This result conforms to the one obtained by T. Oksanen by assuming despotic habitat choice and essentially larger patch sizes. For habitat complexes heavily dominated by the barren habitat, spillover predation was predicted to be weak, as was the case in her large patch model. Unlike in her analysis, however, predation pressure was substantially reduced also within the productive habitat. In habitat complexes where patches are so small that they are exploited in a fine-grained manner, predation pressure was always found to be more intense in the barren habitat, contrary to the predictions of the original model of exploitation ecosystems. This analysis thus suggests that their model is applicable mainly on the landscape level. On the level of individual habitats, the applicability of their results depends on the habitat configuration (at its best for the prevailing habitat of the landscape and for moderate-sized patches of an essentially more productive habitat) and generally decreases with decreasing patch sizes.

Keywords: patch use; predation; productivity; spatial heterogeneity; trophic exploitation

Introduction

According to the hypothesis of exploitation ecosystems (Oksanen *et al.*, 1981; see also Fretwell, 1977) there is a productivity threshold at which population regulation in the vertebrate branch of terrestrial grazing chains changes dramatically. In productive ecosystems the grazing chain has three-link dynamics: herbivores are regulated by carnivores while both carnivore and plant populations are primarily resource-limited, as proposed by Hairston *et al.* (1960). Conversely, on the barren side of the productivity threshold, the grazing chain is predicted to have two-link dynamics: grazing vertebrates are strictly resource-limited and the vegetation is under intense natural grazing pressure. This transition was predicted to be accompanied by a sharp rise in

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above-ground plant biomass, which has actually been observed at the productivity level of about $700 \text{ mg}^{-2}\text{year}^{-1}$, corresponding to the transition from typical tundras to subarctic scrublands and woodlands and from short grass steppes to meadow steppes, tall grass prairies and savannas (Oksanen *et al.*, 1981; Oksanen, 1983; McNaughton, 1985).

When applied to large-scale geographical patterns, the logics of the hypothesis outlined above are straightforward. Assuming spatial heterogeneity in a scale where patches are smaller than maximal dispersal distances but larger than the home ranges of consumers, the model of Oksanen *et al.* (1981) presupposes Fretwell's (1972) ideal-free habitat choice. If habitat choice obeys Fretwell's (1972) ideal-despotic model, consumption will 'spill over' from productive habitats to barren ones (see also Łomnicki, 1978, 1987; Pulliam, 1988; Oksanen, 1990) and the differences in local population dynamics may become substantially weaker or even reversed, as compared with the predictions of Oksanen *et al.* (1981).

In nature, primary productivity may vary in a still smaller scale. This applies especially to subarid habitat complexes, where availability of water varies profoundly over short distances (Walter, 1964, 1968). However, also in subarctic habitat complexes, primary productivity varies by an order of magnitude between adjacent habitat patches (Wielgolaski, 1975). The prevailing, relatively barren habitat types often cover vast areas, whereas patch sizes for more productive habitats usually only range from a few hundreds of square metres to a couple of hectares (Kalliola, 1939; Anon, 1980). Although small herbivorous animals often have home ranges of this size or even smaller, even the least carnivores cover substantially larger areas during their normal, daily movements (Erlinge, 1974, 1977; King 1975; Debrot and Mermod, 1983; Oksanen *et al.*, 1991). Thus carnivores living in areas at the transition between the three-link and two-link ecosystems of Fretwell (1977) and Oksanen *et al.* (1981) will often face a situation where their home ranges or territories consist of an archipelago of favourable patches, embedded in a matrix of barren ground. Nevertheless, the barren habitats harbour some prey. Consequently, predators may be motivated to prey opportunistically on herbivores which are encountered on transit stretches.

Below, we will tentatively analyse the premises and population dynamical consequences of opportunistic predation by transient predators (a more formal treatment will be presented by M. Gyllenberg and T. Oksanen, in preparation). Our main assumptions are as follows. We assume a two-habitat system where the more productive habitat exists as discrete patches, while the less productive one forms a continuous matrix in which the productive patches are embedded. Each habitat harbours a prey species of its own. The prey species occurring on the productive patches is assumed to disperse freely between patches and to choose habitat in a density-dependent manner (Morris, 1988) so that the between-patch differences in prey density created by predator visits are quickly eliminated. We first assume that the patches are so small that predator cannot distinguish between the two habitat types (the case of fine-grained predation). Thereafter, we look at a situation where the patches are large enough to allow active habitat choice but nevertheless smaller than the home ranges of predators (the case of coarse-grained predation). For the sake of tractability, we work with a two-dimensional predator-prey model where the prey has logistic population growth and the predator has type II functional response. (In the neighbourhood of the equilibrium, more complicated situations can normally be approximated by these simple ones.) The consequences of relaxing some of the assumptions will be discussed.

The case of fine-grained predation

Assuming *laissez-faire* exploitation, the predator-prey dynamics within a homogeneous area can be described by means of the following two differential equations:

$$dH/dt = rHg(H) - af(H)HC \tag{1}$$

and

$$dC/dt = -mC + kaf(H)HC \tag{2}$$

where H is prey (herbivore) density, r is the intrinsic growth rate of the prey population, $g(H)$ describes the density-dependence of prey reproduction ($g(H) > 0$ if and only if $H < K$, where K is a positive constant called 'carrying capacity'), a is the intrinsic attack rate of the predator (carnivore), $f(H)$ describes the dependence of the attack rate on prey density, C is predator density, m is the predator mortality in the absence of prey and k is the conversion efficiency of captured prey to the maintenance and reproduction of predators (see Murdoch and Oaten, 1975; Rosenzweig, 1977; Oksanen, 1990).

Setting $dH/dt = 0$, we can solve the zero isocline for the prey as:

$$C^* = \frac{r}{a} \frac{g(H)}{f(H)} \tag{3}$$

where C^* is the carnivore density required to neutralize the growth of the prey population. With logistic prey reproduction and type II functional response in predators, Equation 3 generates the typical, arch-shaped prey isocline (Fig. 1, dashed curve).

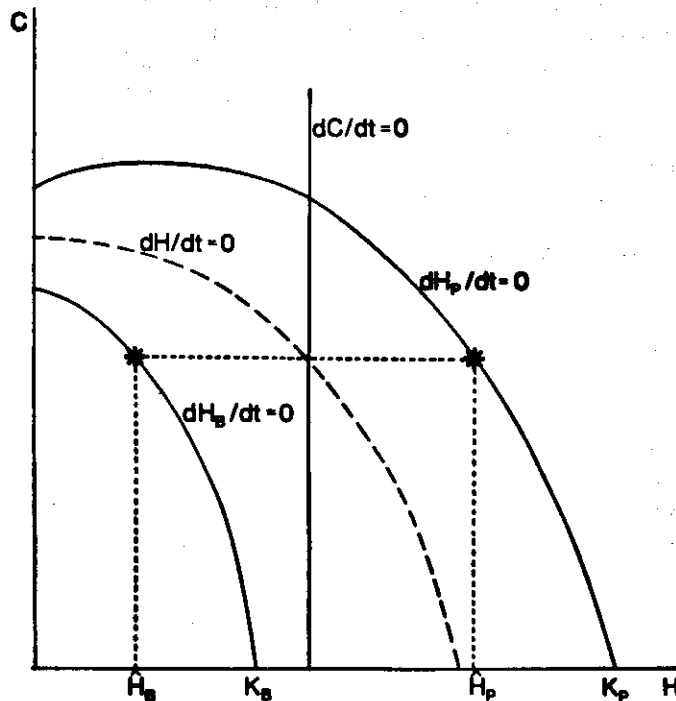


Figure 1. A predator-prey ($C-H$) system for a heterogeneous landscape with fine-grained predation. The dashed prey isocline represents the prey stock within the entire landscape, the solid prey isoclines refer to dynamics within productive patches ($dH_p/dt = 0$) and for barren ones ($dH_b/dt = 0$). The stars stand for equilibria within the two habitats. As predator densities are the same in all habitats, the equilibria are found by moving horizontally from the landscape level equilibrium to the habitat-specific isoclines.

Setting $dC/dt = 0$ we obtain the equation for the carnivore isocline:

$$akf(H^*)H^* = m \quad (4)$$

where H^* refers to the prey density required for zero growth of predators. Notice that C does not occur in Equation 4. Since $f(H)H$ is an increasing function of H , Equation 4 has a unique solution H^* and thus generates a vertical predator isocline (Fig. 1, see also Rosenzweig, 1977).

This set of equations also applies to heterogeneous landscapes where patch sizes are so small that predators cannot exercise any form of habitat choice. Then the above equations represent the landscape perspective or the predator's view of the system. For the predator, the essential thing is the overall encounter rate with the prey, while the dynamics of the pooled prey stock depend on the overall encounter rate between the predator and the prey.

However, individual prey populations are assumed to live within one habitat type or another. Even without notable differences between the life history parameters of the two prey species, their isoclines must be different, owing to the differences in the resource situation and availability of cover. From the point of view of prey populations, there will thus be two different pairs of Equations 1 and 3, one pair for each habitat type, with different parameter values. The equations for the barren habitat will have lower r and K (due to resource shortage) and probably also higher a (due to poor cover). Consequently, the prey isocline for the barren habitat will be contained within the prey isocline for the productive habitat, when the two prey isoclines are superimposed on each other (Fig. 1, solid curves). In this kind of presentation, the prey isocline for the entire landscape will represent the weighted average of the habitat-specific isoclines, weighing factors being the proportions of the landscape consisting of the two habitat types.

If the predator cannot distinguish between the two habitat types, predators will be evenly distributed over the whole landscape. Consequently, the equilibria for the two habitat types can be found by moving horizontally from the pooled prey isocline for the entire landscape (dashed) to the habitat-specific population isoclines (Fig. 1, the movement denoted by dotted lines; the equilibrium points marked by stars). Predation pressure can be defined as the percentage difference between carrying capacity and equilibrium prey density. We immediately see that predation pressure will be more intensive in the barren habitat than in the productive one, contrary to the predictions of Oksanen *et al.* (1981). If the difference between habitat quality is large, there is a distinct possibility that the prey population in the barren habitat will become extinct.

If the same prey species inhabits both habitat types, the prey equations must also contain immigration and emigration terms. Depending on the mechanics of between-habitat movement, several isocline forms can be generated for the two habitats. The most plausible case is net influx of prey from the productive habitat to the barren one. This would tend to lower the prey isocline for the productive habitat and to create a 'chimney' (technical prey refugium) to the prey isocline for the barren habitat (compare with Oksanen, 1990). Then the barren habitat will always contain some prey but it may act as a dispersal sink to which surplus animals come and where they die quickly, unless they find a vacant territory in some productive patch.

Logics of spillover predation in coarse-grained systems

When predators are capable of distinguishing between the two habitats, the situation becomes more complicated. In order to tackle it, we must combine the models of optimal patch use (Charnov, 1976, Parker and Stuart, 1976) with the predator-prey models. This integration requires some unorthodox treatment of both model types. The patch use models usually deal with different kinds of patches, embedded in an empty 'non-habitat'. For us, however, there is just

one patch type and the matrix is not empty. When applying predator-prey models to the set of productive patches, the functional response of predators must be re-defined as the relation between prey density and the average predation rate during a patch use cycle. (Local prey densities decline during each patch use bout. Thus the momentaneous prey density experienced by the predator lacks population dynamical significance for the predator and cannot be predicted from the overall prey density in the productive habitat.)

According to the Charnov-Parker marginal value theorem, the productive patches will be left, when the gain rate within the patch is equal to the average gain rate for both search and pursuit within patches and travelling between them. Opportunistic foraging during transit stretches should be exercised, if the mean gain rate during the act of opportunistic predation (switch from travel to pursuit, the predation itself and return to travel behaviour) exceeds the average gain rate during the entire patch use cycle (Fig. 2), i.e. if the gain of predation exceeds the cost of prolonged travel and switching from transit to pursuit and back to transit behaviour. This condition should normally be trivial for mammals preying on mammals, because the mammalian prey are large and the switching costs are low for animals travelling along the ground surface. The converse situation may apply to birds preying on small invertebrates.

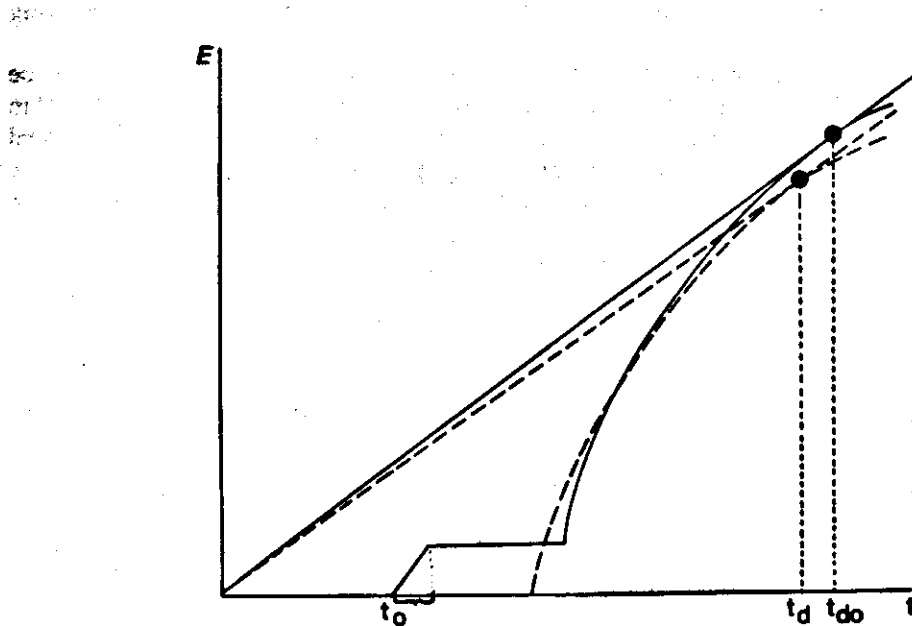


Figure 2. Patch use cycles with (solid lines) and without (dashed lines) opportunistic predation. E = accumulated yield of predation; t = time; t_o = time spent in opportunistic predation; t_d = departure time without opportunistic predation; t_{do} = departure time with opportunistic predation.

Dynamics in a patchy, coarse-grained predator-prey system

In the models of optimal patch use, the accumulated yield of within-patch hunting is assumed to be an increasing function of the time spent in the patch with a horizontal asymptote (Charnov,

1976; Parker and Stuart, 1976; for integration of patch use and competition models, see Brown and Rosenzweig, 1986). We shall explicitly assume that this function is given by:

$$E = A(1 - e^{-ct}) \quad (5)$$

where t denotes time spent in the patch and c is a measure of the within-patch hunting efficiency. (This choice of energy yield function means that we in fact assume a type I functional response for within-patch predation. For short handling times Equation 5 is a good approximation to the energy yield function corresponding to a type II functional response.) During the patch-use bout of a predator, the prey stock is thus gradually depleted, and continued hunting effort yields successively fewer and fewer prey per time unit. The asymptote $E = A$ of the yield curve represents the yield that could theoretically be extracted by totally depleting the patch. In the literature, the term 'patch quality' usually refers to the initial gain rate of a predator which has just entered the patch or to the height A of the asymptote. Of course, the two are closely interrelated. Differentiating Equation 5 with respect to time and evaluating at $t = 0$ one sees that the initial gain rate $E'(0)$ equals cA . Patch productivity, in turn, refers to the primary productivity of the patch which determines the carrying capacity K of the patch for the prey. Thus patch productivity can be identified with K and interpreted as the supremum of patch quality A , obtained when the patch has been fallow for a long time so that the prey stock is at carrying capacity.

The average gain rate for a system where the predator population is at equilibrium can be deduced from Equation 4 which is satisfied when the average gain rate of a predator ($kaf(H)H$ in Equation 4) is equal to m . (As noted above, the term representing the predator's functional response, $af(H)H$, must now be interpreted as the average predation rate during the patch use cycle.) At equilibrium, the average gain rate will thus be constant, regardless of the configuration of the habitat complex and the productivity of individual habitat patches. If the productive patches are close to each other, their average quality will be low at equilibrium, whereas long

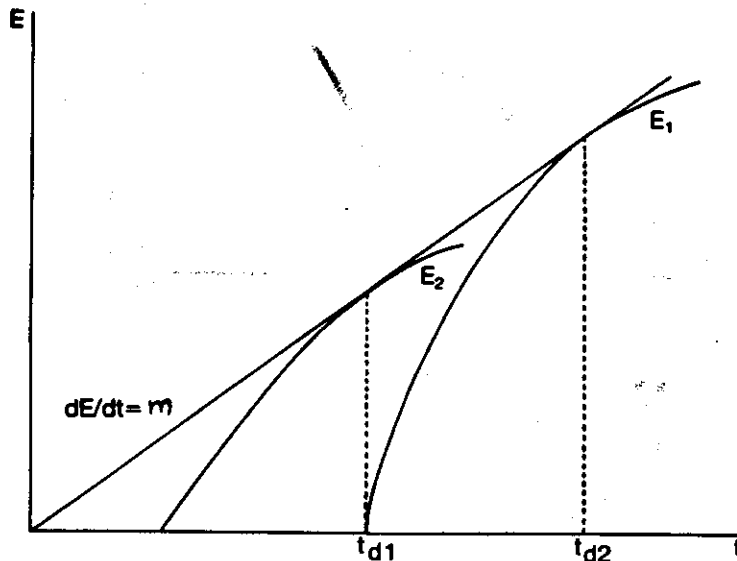


Figure 3. Yield curves for a habitat complex with short transit times (E_1 , departure time t_{d1}) and for a habitat complex with long transit times (E_2 , departure time t_{d2}), assuming identical patch productivities and predator populations which are at their population dynamic equilibria.

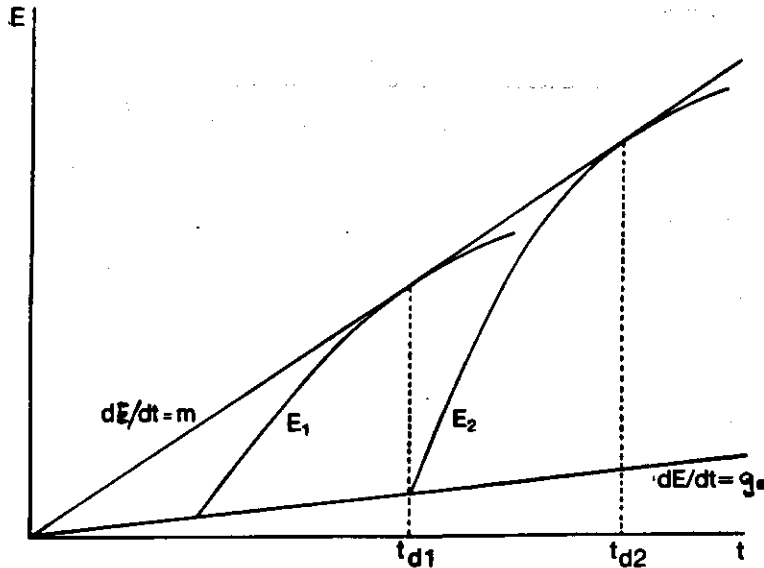


Figure 4. As Fig. 3, but assuming a positive gain rate (g_0) in the barren habitat due to opportunistic predation.

transit distances create a situation where the average quality of productive patches will be high at equilibrium (Fig. 3). If opportunistic predation in the transit habitat yields substantial amounts of energy, the rate at which patch quality is improved by long transit distances is slower, but the principle is nevertheless the same (Fig. 4).

The mechanism connecting patch quality to transit distances lies in the dynamics of the predator population. If productive patches suddenly disappear from a system, the quality of the remaining patches will, in the short run, decrease (as all predators now concentrate their foraging activity to the remaining productive patches). However, the average gain rate of predators will then drop below m , which will initiate a decline in predator numbers. A new equilibrium will be found when the average prey density within the remaining productive patches is high enough to allow predators to compensate for the increased transit distances or when the predators have become extinct. The latter alternative becomes relevant if patch productivity is too low to allow a sufficient increase in patch quality.

The relation between patch quality and transit time and its influence on the ratio of predator density in the productive habitat to predator density in the barren one can be analysed using the Charnov-Parker marginal value theorem. Let T_B and T_P denote the average transit time (time spent by a predator in the barren habitat) and the time spent by a predator in the productive habitat, respectively. The total energy E gained on average by a predator is as a function of time given by:

$$E = mt, t \geq 0 \tag{6}$$

It follows from Equation 5 that when the predator has arrived at a productive patch at time $t = T_B$ it will gain energy according to

$$E = A(1 - e^{-c(t-T_B)}), t \geq T_B \tag{7}$$

By the Charnov-Parker marginal value theorem the optimal time T_P the predator spends in the

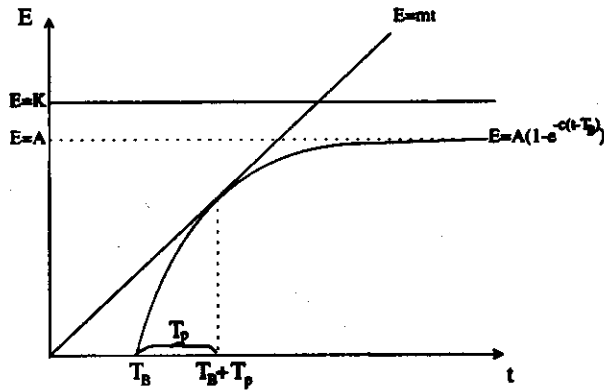


Figure 5. The average energy yield function $E = mt$, and the within-patch energy yield function $E = A(1 - e^{-c(t-T_B)})$. m is the average energy gain rate, c is the within-patch hunting efficiency and T_B is the average transit time. The optimal time T_P a predator spends in a productive patch is determined by the condition that the two curves are tangent at $t = T_B + T_P$.

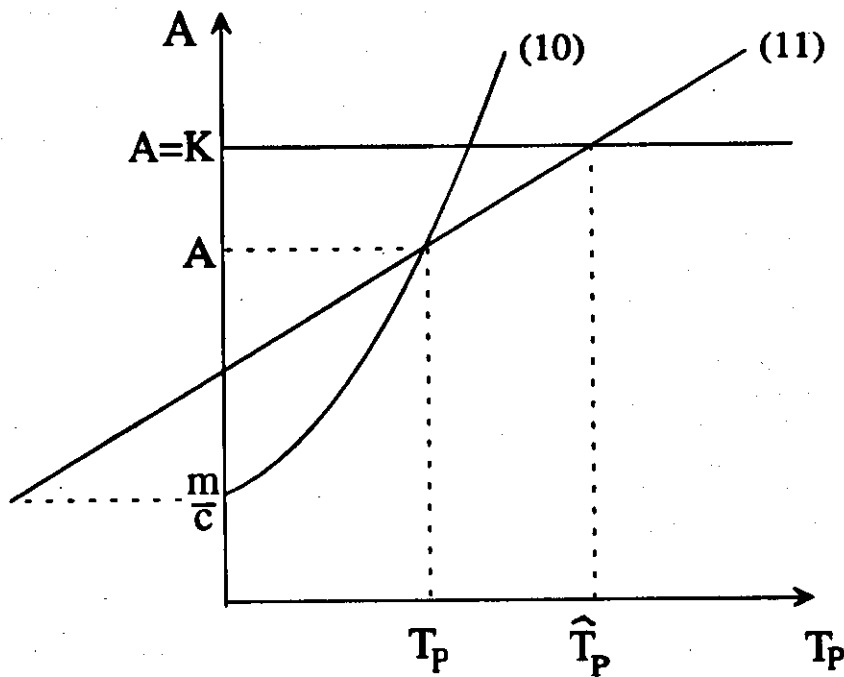


Figure 6. The graphs of the functions determined by Equations 10 and 11. The point of intersection gives the solution (T_P, A) .

productive habitat is determined by the condition that the curve (represented by Equation 7) and the straight line (represented by Equation 6) are tangent at $t = T_B + T_P$ (Fig. 5).

Since the curves (represented by Equations 6 and 7) coincide at $t = T_B + T_P$ one has

$$A(1 - e^{-cT_P}) = m(T_B + T_P) \quad (8)$$

and since they have the same derivative at $t = T_B + T_P$ one has

$$cAe^{-cT_P} = m \quad (9)$$

Equation 9 yields

$$A = \frac{m}{c} e^{cT_P} \quad (10)$$

Substituting Equation 10 into Equation 8 one obtains

$$A = m(T_B + T_P) + \frac{m}{c} \quad (11)$$

The Equations 10 and 11 represent two curves in the (T_P, A) -plane. The point of intersection gives the solution (T_P, A) (Fig. 6).

Since A has to be less than or equal to K (recall that K is the supremum of admissible A -values), it follows from Equation 11 that T_P has to be less than or equal to \hat{T}_P defined by

$$\hat{T}_P = \frac{K}{m} - \frac{1}{c} - T_B \quad (12)$$

If the solution to Equation 10, Equation 11 has $T_P > \hat{T}_P$, then the predator species will become extinct. From Equation 12 we infer that a necessary condition for the species to persist is

$$\frac{cK}{m} > 1 \quad (13)$$

If Condition 13 does not hold, then both the quality and productivity of the 'productive' habitat are low, in other words the habitat is in fact barren! So let us assume that Condition 13 holds. The species persists, that is, $T_P \leq \hat{T}_P$ if and only if

$$\frac{m}{c} e^{c\hat{T}_P} \geq K \quad (14)$$

Substituting Equation 12 into Condition 14 and taking logarithms the condition takes the form

$$\frac{cK}{m} - 1 - cT_B \geq \log\left(\frac{cK}{m}\right) \quad (15)$$

By Condition 13, Condition 15 holds for $T_B = 0$. As cT_B increases cK/m has to increase in order to allow the species persist (Fig. 7).

Given a geographical pattern, that is, a distribution of productive patches, the average transit time T_B can be determined. As the fraction p of the landscape covered by the productive habitat increases the average transit time T_B decreases. With constant patch size and even distribution of productive patches, T_B scales roughly with the square root of p , because it takes the removal of three-quarters of productive patches to double between-patch distances. Condition 15 then gives a relation between the productivity of the patches (carrying capacity K), the hunting efficiency (relative rate of energy gain within patches, c), and the average gain rate at equilibrium (m) which determines whether the species will become extinct or not. Figure 7 illustrates this.

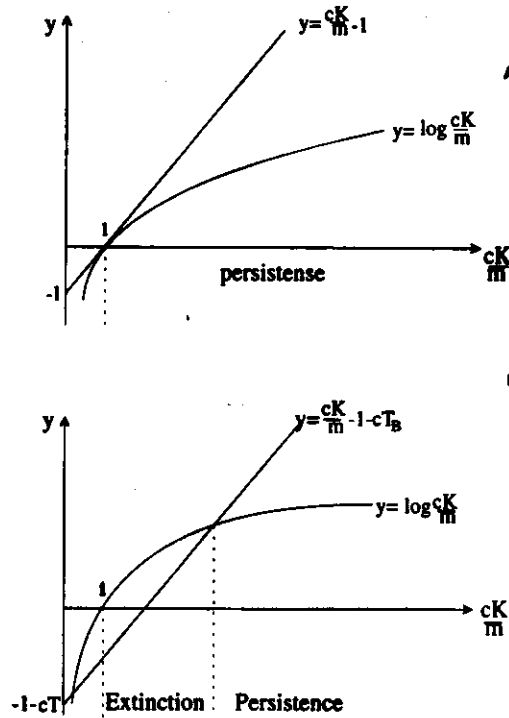


Figure 7. The curves $y = cK/m - 1 - cT_B$ and $y = \log(cK/m)$ for (a) $T_B = 0$ and (b) $T_B > 0$. The species persist for parameter values where the former curve is above the latter. Observe that our model applies only to parameter values for which $cK/m > 0$.

Let us now turn to the question concerning the fraction of individuals in the barren habitat. At equilibrium this fraction is given by

$$q = \frac{T_B}{(T_B + T_P)} \quad (16)$$

It follows from Equation 10 and Equation 11 that q satisfies the equation

$$q(e^{-cT_B} e^{-\frac{cT_B}{q}} - 1) = cT_B \quad (17)$$

Observe that q depends only on the product of c and T_B , that is the hunting efficiency and the transit time.

Equation 17 is a transcendental equation and cannot be solved explicitly. However it can be proved using the implicit function theorem that Equation 17 defines a function $q = q(cT_B)$. Equation 17 was solved numerically and the function $q = q(cT_B)$ is plotted in Fig. 8. As seen from Fig. 8, q increases with increases in T_B in a nonlinear manner. In landscapes with relatively low values of T_B (i.e. the productive habitat covers a large part of the landscape) q is very sensitive to changes in T_B . As the predominance of the barren habitat increases, an increasing fraction of the predator population will be in the barren habitat. Thus predator densities stay at roughly similar levels in both habitats. Conversely, in landscapes with large T_B (i.e. the barren habitat

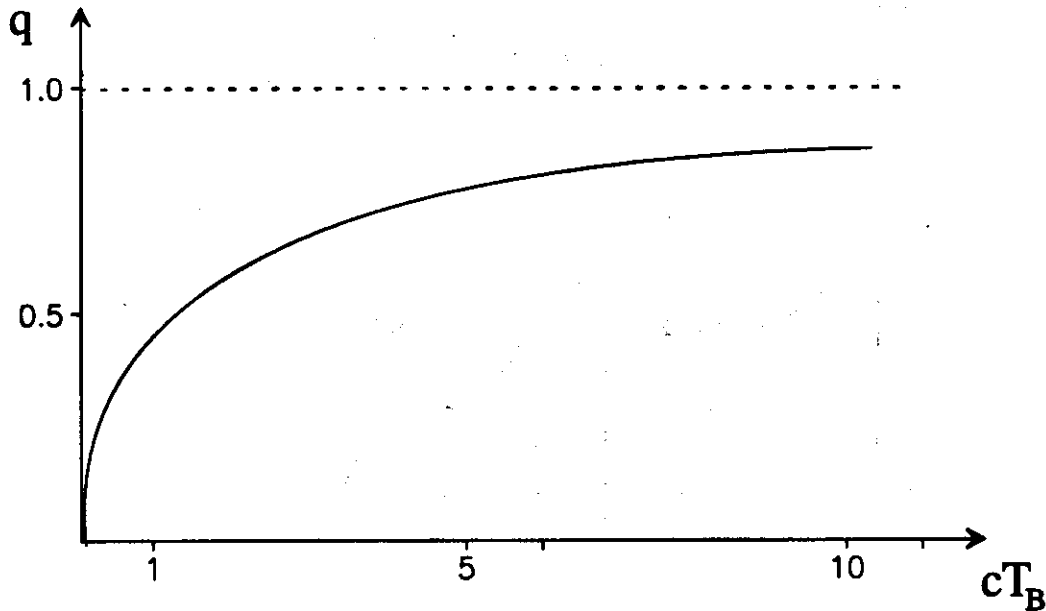


Figure 8. The fraction q of individuals in the barren habitat as a function of cT_B , that is the product of the within-patch hunting efficiency and the average transit time.

overwhelmingly prevails) further increase in T_B has very little impact on the distribution of predator numbers between the two habitats. As increasing T_B is accompanied by a reduction in the fraction of the landscape by the productive habitat, the consequence is that predator densities become increasingly dissimilar in the two habitat types. The few productive patches may still experience rather high predator densities, whereas in the predominating barren habitat predator densities are diluted to negligible level.

In terms of predator-prey models, the abundances of the two habitat types determine the course of the landscape-level prey isocline (which answers the question what predator density in the landscape is sufficient to neutralize the growth of the pooled prey stock). In systems where productive habitats abound, this isocline will run close to the isocline for the productive habitat. The equilibrium density of predators will be high and predators will be rather evenly distributed between the two habitats. Thus depending on the productivity of the barren habitat, predation pressure is likely to be similar in both habitat types (Fig. 9) or more intense in the barren habitat. If the barren habitat is barren enough, its prey species will be eliminated by predation (Fig. 10). Thereafter, the barren habitat is likely to become a dispersal sink for the prey populations of productive patches.

In landscapes where the barren habitat prevail heavily, the landscape-level prey isocline closely follows the prey isocline for the barren habitat. Predator densities in the landscape as a whole will be low and the between-habitat distribution of predators will be very uneven (Fig. 11). Consequently, predation pressure in the barren habitat will be negligible and prey densities will be close to the carrying capacity. Even for the productive habitat, only moderate predation pressure is predicted, because patch quality must be high enough to compensate for long travel distances.

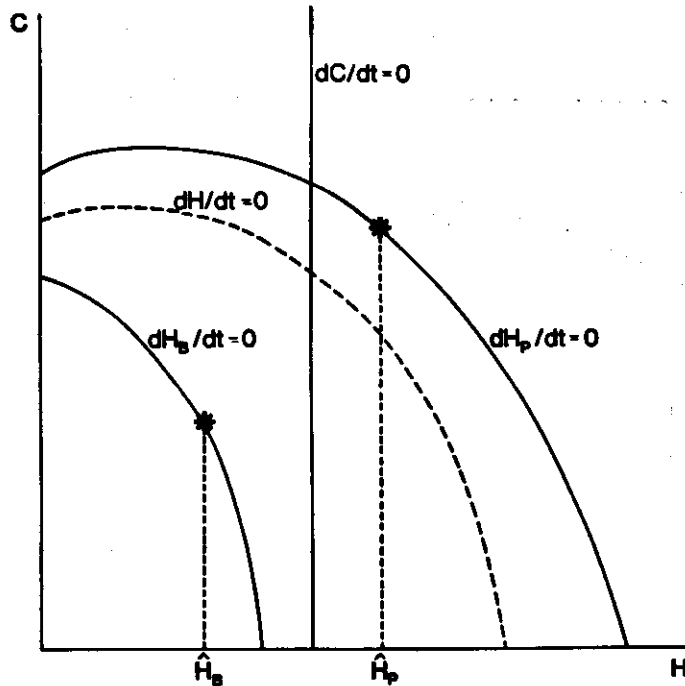


Figure 9. A predator-prey ($C - H$) system for a heterogeneous landscape with coarse-grained predation, assuming that a large part of the landscape consists of the productive habitat. The dashed prey isocline represents the prey metapopulation within the entire landscape, the solid prey isoclines refer to dynamics within productive patches ($dH_p/dt = 0$) and barren ones ($dH_b/dt = 0$). The stars stand for equilibria within the two habitats, found by dividing the metapopulation equilibrium predator population between the two habitats in accordance to the predictions of the patch use model.

Relaxing some assumptions

If the system is characterized by a stable equilibrium, prey densities in the barren matrix habitat may really stay at the level predicted by Fig. 1 and Figs 9–11. In the productive habitat, corresponding equilibrium unquestionably exists for large sets of habitat patches. For individual patches, the equilibrium approach is critically dependent on the assumption that between-patch dispersal quickly reshuffles prey numbers within a fairly large set of patches after each patch use bout of the predator. If rates of between-patch dispersal are low and patch recovery chiefly takes place by means of local population growth, the equilibrium approach will be grossly unrealistic in a local perspective. Within each individual patch, prey densities then range from carrying capacity to the departure density, depending on the time elapsed from the latest predator visit. In such a system, the isocline concept becomes a primarily heuristic one and has little to do with local predator-prey dynamics. Each patch is characterized by strongly non-equilibrium dynamics, and isoclines exist only for large sets of habitat patches.

In systems where patch quality varies owing to differences in the degree of recovery between individual patches, predators experience stochasticity which is absent from systems with efficient between-patch prey dispersal. With good luck, a predator hits a patch which has been missed for a long time and thus has its prey population at carrying capacity. With bad luck, a predator may enter a patch which has just been left by another one and where the prey numbers are too low to

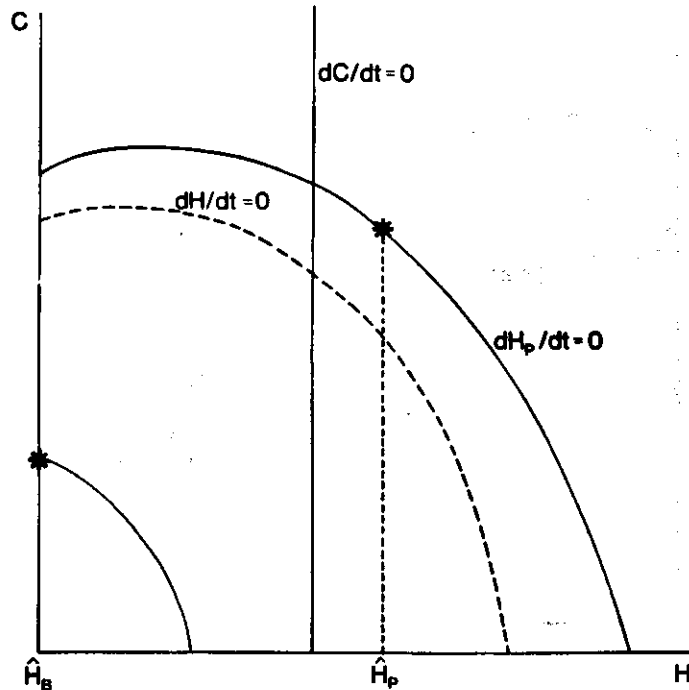


Figure 10. As Fig. 9, but with a barren habitat which is still less productive than in Fig. 9. Now, the barren habitat will, at equilibrium, have no prey at all.

make active patch use profitable. Such uncertainty is likely to increase the costs of transition and to reduce predator numbers in the landscape as a whole.

For a predator, genuine differences between the productivity of different patches are just another source of variation in patch quality. For the prey, in turn, such differences lead to a situation which resembles Rosenzweig's (1971) Paradox of Enrichment. Regardless of its productivity, each patch is left when the within-patch gain rate equals the mean gain rate in the whole landscape (Charnov, 1976). Thus the minimum prey densities will be just the same for all actively exploited patches, regardless of their productivity. This implies longer stay times of predators and higher mortality rates of prey within more productive patches. In this case, the ideas of Rosenzweig (1971) and Oksanen *et al.* (1981) are thus applicable to local differences in predation pressure within a landscape with small-scale habitat heterogeneity.

In systems where the predator-prey equilibrium is locally unstable and thus acts as the focal point of a stable limit cycle, discussions of equilibrium dynamics have little to do with the reality. When predator populations go up and down, their average gain rate (the tangent in Figs 3 and 4) will sometimes exceed m by a wide margin and sometimes fall short of m . During periods of high average gain rate, predators can be expected to be very selective with regards to patch quality. Conversely, during periods of low average gain rate, predators should be much more catholic in their habitat choice. When the prey stock in the productive patches has been depleted to the level that prevails in the barren transitory habitat, predators should abandon their habitat preferences altogether and start hunting actively even in the barren habitat, which indeed seems to be the case (Oksanen *et al.*, 1992).

A final assumption to be relaxed pertains to the trophic structure. We have worked with a two-

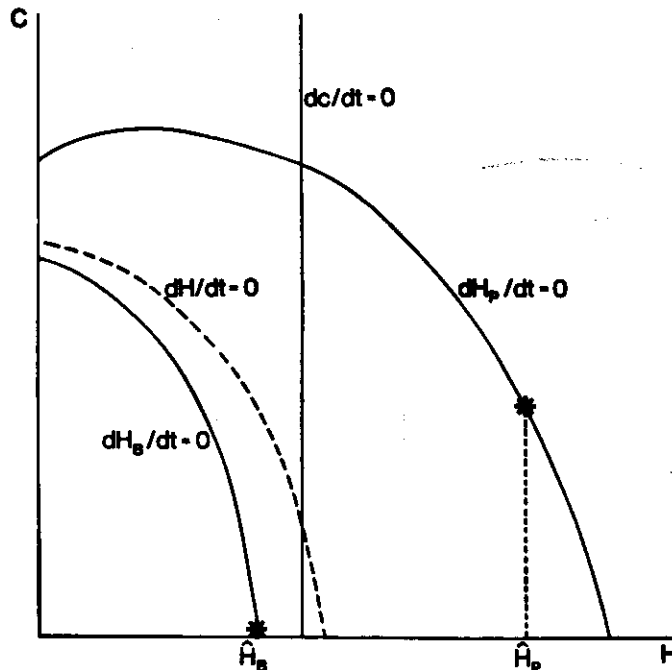


Figure 11. As Fig. 9, but assuming that the barren habitat overwhelmingly prevails. The prey meta-population isocline now runs close to the prey isocline for the barren habitat. The equilibrium predator density in the landscape is low and predator activity is very unevenly divided between the two habitats. Consequently, substantial impact of predation is only felt within the productive habitat.

link model, where prey is assumed to have logistic population growth. We agree with Rosenzweig (1973) and Oksanen *et al.* (1981) that this assumption is most realistic for pure herbivore–plant systems. Predator–prey systems with herbivores in the role of the prey are actually three-link exploitation systems for which the predictions of two-dimensional models are only partially realistic. The main shortcoming of two-dimensional models refers to the dynamics of the prey population in the absence of predators. Two-dimensional models predict that the prey population smoothly approaches carrying capacity. However, this ignores the fact that herbivores are predators of plants and may overexploit the vegetation. If such overexploitation occurs, systems with little or no predation will have violent grazer–plant fluctuations. Moderate intensities of spillover predation may stabilize such systems and will lead to increased equilibrium numbers of the prey (Oksanen, 1990).

Discussion

The small-patch model preliminarily analysed here has both similarities with and differences from the large-patch model analysed by Oksanen (1990). In both cases, spillover predation may or may not be created, but the necessary and sufficient conditions are entirely different. In the large-patch model, the critical condition is despotic habitat choice. In the small-patch model, in turn, spillover predation requires that opportunistic predation is profitable. In both cases, spillover predation can become substantial only if a fairly large percentage of the landscape consists of the productive habitat. Otherwise, spillover predation will be so heavily diluted that its impact will be negligible.

Another similarity refers to the relationship between two prey species, each specialized to one habitat type. Even if they never meet, their relationship can be characterized as apparent competition (Holt, 1977, 1984). In the small-patch model analysed above, the prey within the productive habitat generate opportunistic predation in a habitat which, by itself, would not have any predators at all. Conversely, the presence of some prey in the barren habitat reduces the costs of travel and thus increases predation pressure within the productive habitat. Increase in the abundance of prey within one habitat type may temporarily reduce predation pressure in the other one, but after the predators have reached their new equilibrium, the net result will always be increased predation pressure. In the large-patch model analysed by Oksanen (1990) a similar relation is generated via the impact of prey numbers on the emigration and survival rates of predators. (Higher prey numbers in the productive habitat imply higher predator densities and thus higher rates of predator emigration to the barren habitat. Higher prey numbers in the barren habitat, in turn, boost the survival rates of predators and thus increase the rate of return migration from the barren habitat to the productive one.)

The main difference pertains to productive habitats. In the large-patch case, the availability of barren habitat has some impact on the dynamics within the productive habitat. Weak individuals are likely to prefer an uncertain fate in the barren habitat to an almost certain death in the productive one (Łomnicki, 1978, 1987), which will somewhat reduce equilibrium predator density and prey depletion in the productive habitat (Oksanen, 1990). However, this is a very minor impact compared with the dramatic reduction of predator numbers – possibly even total extinction of predators from the entire landscape – predicted by the small-patch model for habitat complexes where the barren habitat heavily prevails. Also the mechanism is totally different. In the large-patch model, the availability of barren habitat is an opportunity for weak individuals and leads to higher predator densities on the landscape level than would be the case if the opportunity were not exploited (see also Holt, 1985). Conversely, in the small-patch model, the barren habitat is a cost for all individuals and leads to lower predator densities in the landscape than would be the case if all productive patches were concentrated to a single area.

The case of fine-grained predation (Fig. 1) can be regarded as the most extreme variant of the small-patch model. When habitat choice is not possible, the costs due to the presence of the barren habitat are maximally high. Moreover, with fine-grained predation, local differences in predation pressure are always diametrically opposite to those predicted by Oksanen *et al.* (1981): the more productive the habitat, the lighter the predation pressure. The model of Oksanen *et al.* (1981) then only works in comparisons between different landscapes, never within the landscape.

Although our focus has been on carnivore-herbivore interactions at the transition between three-link and two-link ecosystems, the same principles hold for herbivore-plant interactions at the transition between two-link and one-link systems (e.g. from the high-arctic tundra to the polar desert), and for such systems, the interpretation of two-dimensional models is straightforward. The spatial scale to which the above analysis then applies depends on the mobility of the key grazers. In systems dominated by small mammals, the small-patch model works in the scale of a few metres only. However, in ungulate-dominated systems, the small-patch model can be expected to be applicable in the spatial scale of several kilometres. Thus in order to find genuine one-link systems where plants are not influenced by vertebrate herbivory, it may be necessary to work several kilometres away from the nearest substantial area with a continuous plant cover.

Acknowledgements

We are grateful to the thoughtful comments of Joel Brown and Douglas Morris. The figures were drawn by Görel Marklund. The study was supported by grants from Naturvetenskapliga Forskningsrådet (NFR).

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