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THE TIME-SCALE PROBLEM IN EXPLOITER-VICTIM MODELS: DOES THE SOLUTION LIE IN RATIO-DEPENDENT EXPLOITATION?

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Abstract.—Standard exploiter-victim models assume an instantaneous connection between foraging and population dynamics. However, in nature this connection is inevitably time-delayed: it takes time to convert food into offspring. R. Arditi and L. R. Ginzburg proposed that this time delay implies ratio-dependent exploitation. Models with ratio-dependent exploitation predict that primary productivity has no impact on food chain length and that the standing crop of all trophic levels increases linearly with increasing primary productivity. Conversely, the traditional victim-dependent models imply that food chain length increases with increasing primary productivity and that only top trophic levels and trophic levels that are an even number of links below the top respond positively to increasing primary productivity. We study the impact of time-delayed numerical responses on predator isoclines, and we do not find support of the theoretical arguments of Arditi and Ginzburg. We also review data on biomass patterns in plants and herbivores, which seem to support the predictions of the victim-dependent model.

When modeling interactions between exploiters and victims, it is customary to assume that resources consumed by the exploiter have an immediate impact on population dynamics of both exploiters and victims (Rosenzweig and MacArthur 1963; Rosenzweig 1971, 1977; Noy-Meir 1975; Tanner 1975; Caughley and Lawton 1981). In systems without interference (i.e., laissez-faire systems), this implies that the per capita rate of change in exploiter populations only depends on the absolute density of the victims. The number of victims per exploiter has no significance whatever. In the terms of isocline models, this translates to a vertical predator isocline in laissez-faire exploitation systems. Isoclines with a positive slope imply feeding interference, agonistic behavior, or spatial heterogeneity (Hassel and May 1974; Beddington 1975; Murdoch and Oaten 1975; Hassel 1981).

The logics behind the vertical exploiter isocline have been hard to communicate. Even in modern textbooks, one can find arguments of the following type: "The predator zero isocline in the Lotka-Volterra model is vertical. This means that the same number of prey is assumed to be sufficient to just maintain *any* number of predators, which is most unlikely. It is much more likely that larger numbers of populations require larger populations of prey to maintain them" (Begon et al. 1990, p. 344, italics in original). The counterargument of Rosenzweig (1977) is that the model deals with instantaneous rates of change. In the long run, larger numbers of predators do indeed need more prey, because they will quickly reduce the prey stock. However, when this has happened, the system has moved

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across the predator isocline. Thus, Rosenzweig (1977) dismisses the argument of more predators needing more prey as a conceptual confusion between the location of the exploiter isocline and the rate at which it is approached in situations with different exploiter densities.

Although solidly based on the theory of differential equations, Rosenzweig's (1977) reasoning is biologically problematic. Arditi and Ginzburg (1989) point out that Rosenzweig assumes an instantaneous connection between foraging and population dynamics. In nature, however, this connection is inevitably time-delayed. Converting food into a clutch of weaned offspring takes time, and well-fed exploiters can miss several meals without facing the threat of immediate starvation.

Arditi and Ginzburg (1989) propose that, in the population-dynamical time scale, the functional response of exploiters depends on the density of victims per exploiter, not on the absolute density of victims. As compared with the "prey-dependent" models of Rosenzweig (which will be called victim-dependent for the sake of generality), the model of Arditi and Ginzburg leads to entirely different predictions on population dynamics and patterns of exploiter and victim abundances. Below, we will review the predictions of the two classes of models and propose two alternative ways to incorporate the time delay in the numerical response of exploiters in exploiter-victim models. Finally, we will discuss the relation of the different models to data.

THE IMPACT OF ENRICHMENT ON TROPHIC DYNAMICS

A simplified illustration on the reaction of a purely exploitative laissez-faire three-trophic-level (carnivore-herbivore-plant) model to increased primary productivity is presented in figure 1 (derived from the model of Oksanen et al. 1981; increased primary productivity is represented by the successive expansion of the arch-shaped plant isoclines in fig. 1). The model predicts that there are three different zones within which trophic dynamics show entirely different responses to enrichment.

These predictions are summarized in figure 2. Extremely barren "one-link" ecosystems (Zone I) are devoid of mobile grazers. Thus, plant biomass increases linearly with increasing primary productivity. Somewhat more productive "two-link" ecosystems (Zone II) harbor mobile grazers but no persistent populations of efficient carnivores. Aboveground plant biomass remains fixed at the hunger threshold of the grazers, and increased primary productivity only leads to higher grazer densities (as predicted by Rosenzweig's [1971] "paradox of enrichment"). In still more productive "three-link" ecosystems (Zone III), grazers become regulated by carnivores and grazer biomass becomes locked at the carnivore isocline. Plant biomass first "jumps" to an essentially higher level (as carnivores prevent overgrazing) and then starts to increase roughly linearly with increasing primary productivity. Carnivore biomass increases first sharply and thereafter in a decelerating manner, as the turnover rate of herbivore populations starts to be limited by their physiological capacity to produce offspring. In aquatic ecosystems, secondary carnivores can enter before the increasing trend in primary carnivores

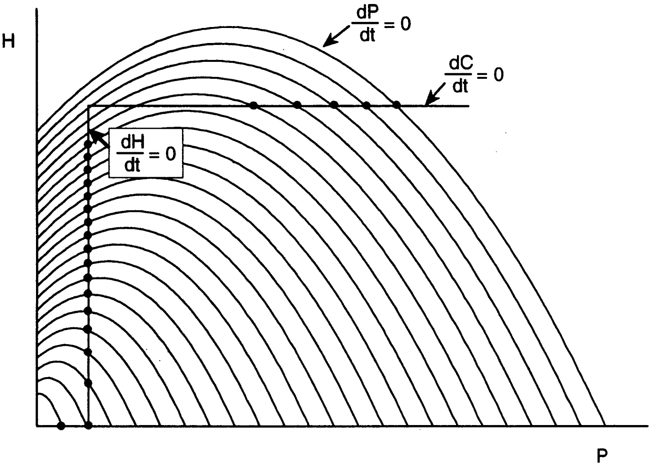

FIG. 1.—A two-dimensional projection of the carnivore-herbivore-plant model of Oksanen et al. (1981) for systems with different primary productivities, reflected in the size and curvature of plant isoclines (the *arch-shaped lines*). The *vertical line* represents the herbivore isocline in the plane defined by plant (*P*) and herbivore (*H*) axes. The *horizontal line* is the projection of the carnivore isocline. The equilibrium points for each system are depicted by *dots*.

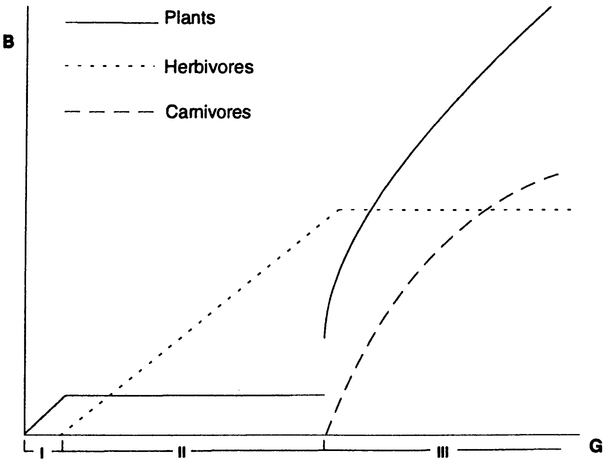

FIG. 2.—The relation of biomass (*B*) of plants, herbivores, and carnivores to potential primary productivity (*G*), which is derived from the model of Oksanen et al. (1981). (Notice different scales for different trophic levels.) The *roman numbers* along the *horizontal axis* refer to the numbers of interacting trophic levels within a given range of primary productivities.

has leveled off. Then, the pattern changes once more: primary carnivore biomass is locked at the hunger threshold of secondary carnivores, herbivore biomass starts to increase, and plant biomass first decreases and thereafter stays constant.

Adding more realism to the assumptions changes many details (Persson et al. 1988; L. Oksanen 1990*a,* 1992; T. Oksanen 1990; Abrams 1993) but has little impact on predictions concerning large-scale geographical patterns in terrestrial ecosystems, unless extreme levels of interference or heterogeneity are assumed. At the most, the plateaus of figure 2 can be somewhat tilted so that all trophic levels will show some positive response to increased primary productivity. However, plants of two-link ecosystems are nevertheless under intense natural grazing pressure that is relaxed in three-link ecosystems. The converse holds for herbivores that are strictly resource-limited in barren two-link ecosystems and chiefly regulated by predators in more productive three-link ecosystems. This pattern of changed trophic dynamics along gradients of primary productivity is central to the reasoning of Fretwell (1977, 1987), Oksanen et al. (1981) and Oksanen (1988, 1990*a,* 1990*b,* 1991), whereas the prediction of exact constancy of biomass is a relatively peripheral technical detail.

As compared to victim-dependent models, the Arditi-Ginzburg model of ratio-dependent exploitation leads to radically different predictions. Exploiters are predicted to be extremely efficient when their own densities are low. Thus, the exploiter isocline is predicted to have a positive slope. Moreover, both exploiter and victim isoclines are predicted to go through the origin (fig. 3, *solid lines*). All trophic levels are predicted to be present even in practically sterile areas, although at very low densities. Increased primary productivity is predicted to lead to a linear increase in the equilibrium biomass at all trophic levels (fig. 4).

TIME LAGS IN EXPLOITER-VICTIM INTERACTIONS

Arditi and Ginzburg (1989) derive their rationale for ratio-dependent exploitation from the discussion of Wiens et al. (1986) concerning interactions between coyotes and jackrabbits. After admitting that daily foraging rates of coyotes are probably determined by the absolute density of rabbits, Arditi and Ginzburg make the following statement: "However, when calculated on the yearly time scale of population dynamics, intuition suggests that the feeding rate should take account of predator abundance: over a year there will be less food available for each coyote (unless food is not limiting). Whatever the behavioral mechanisms are, the final outcome must reflect the fact that, for a given number of prey, each predator's share is reduced if more predators are present. This suggests that the yearly consumption rate should be a function of prey abundance per capita" (Arditi and Ginzburg 1989, p. 312).

There are two major problems with the argument of Arditi and Ginzburg. First, the yearly consumption rates are not derived in a mechanistic way from daily consumption rates. Thus, a colleague who does not share their intuition has difficulties in trying to check the underlying logic. Second, after having stated that they operate within the slow time scale of population dynamics, Arditi and Ginzburg nevertheless work with differential equations. However, differential equa-

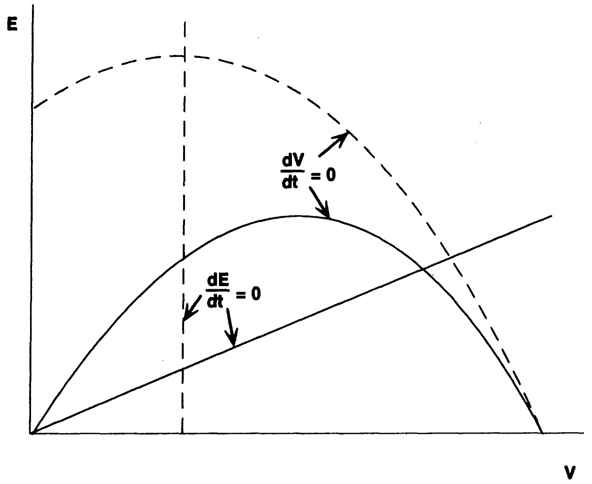

FIG. 3.—Exploiter-victim model (*E*, exploiter; *V*, victim) according to the Arditi-Ginzburg approach of ratio-dependent exploitation. Isoclines for a corresponding system with victim-dependent exploitation are depicted as *dashed lines*.

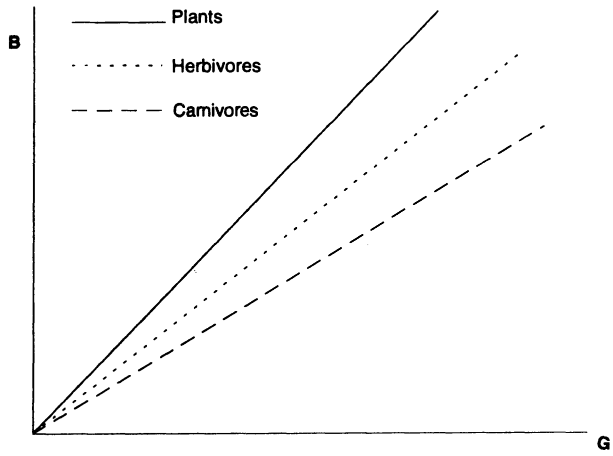

FIG. 4.—The relationship of biomass (*B*) of plants, herbivores, and carnivores to potential primary productivity (*G*), on the basis of the ratio-dependent model (Arditi and Ginzburg 1989, table 2).

tions only deal with instantaneous rates of change. Thus, it is mathematically incorrect to write dN/dt on the left-hand side of an equation and then construct the right-hand side from arguments referring to numerical changes over a long time. One must either stick to instantaneous rates of change or switch from differential equations to difference equations.

Let us start from the more simple case of instantaneous rates of change. Recall that the structure of victim-dependent, laissez-faire exploitation models can be represented by the following pair of equations:

$$\frac{dV}{dt} = rVg(V) - \alpha f(V)VE \tag{1}$$

and

$$\frac{dE}{dt} = -mE + q\alpha f(V)VE, \tag{2}$$

where V and E are population densities of victims and exploiters, respectively, r is the intrinsic growth rate of the victim population, $g(V)$ is the density dependency of victim population's growth, α is the maximum attack rate of exploiters, $f(V)$ describes the way attack rates depend on victim density, m is the mortality rate of starving exploiters, and q is the efficiency with which exploiters convert captured victims to energy for maintenance and reproduction.

Setting $dV/dt = 0$, we can derive the zero isocline for victims as the equation

$$E^* = \frac{r}{\alpha} \cdot \frac{g(V)}{f(V)}, \tag{3}$$

where E^* refers to the exploiter density needed to keep the reproduction and predation rates of the victim in balance. Setting $dE/dt = 0$, we obtain the equation for the exploiter isocline

$$V^* = \frac{m}{q\alpha f(V^*)}, \tag{4}$$

where V^* refers to the victim density required for zero growth of exploiters and $f(V^*)$ refers to the attack rate function, evaluated at $V = V^*$. As exploiter density cancels, equation (4) generates the standard vertical exploiter isocline.

Next, assume that the instantaneous rate of change of exploiters does not only depend on instantaneous feeding rates but is a function of their feeding history. Of course, this has no impact on equations (1) and (3), which describe dynamics of the victim. For the victim, predation does not create a time-scale problem, because deaths have an immediate impact on population dynamics. In equation (2), however, the term $q\alpha f(V)V$ must be replaced by the integral

$$\int_{t_f}^{t_0} q\alpha f(V_t)\, V_t F(t)\, dt,$$

where t_0 refers to the present time, t_f refers to the furthest time in the past from which foraging still has an impact on current population growth, V_t is the victim density at time t, and $F(t)$ stands for the relative contribution of food ingested t time units ago to current population growth, and

$$\int_{t_f}^{t_0} F(t)\, dt = 1.$$

In principle, the feeding history of the victim also influences exploiter-victim dynamics, unless the victim is a plant that immediately converts photosynthetic products to growth. However, equation (1) is phenomenological and does not contain any explicit feeding terms. Thus, the most profitable way to include the feeding history of the prey is to work on three-dimensional exploitation models that explicitly deal with the interaction between the prey and its resources (Rosenzweig 1973; Wollkind 1976; Oksanen et al. 1981). One of us has previously performed such an analysis (L. Oksanen, unpublished analysis), and some preliminary results will be mentioned below.

The above-described change of equation (2) makes the model analytically intractable. However, qualitative conclusions can nevertheless be drawn. If victim numbers stay unchanged, the structural change of the exploiter equation has no impact on population dynamics, because past feeding rates have been equal to the present one. Thus, no matter how they are weighted by the function $F(t)$, the population behaves just as if its dynamics would only depend on current feeding rates. If victim numbers are increasing, then past feeding rates were lower than current ones and the exploiter isocline lies further to the right than in the conventional model (exploiters require more food because of their low energy reserves). Conversely, if victim numbers are decreasing, then past feeding rates were higher than current ones, and exploiters can maintain positive growth rate at lower victim densities than predicted by the conventional model (because exploiters can use fat reserves accumulated during better times).

The exploiter and victim isoclines for a model with time-delayed numerical response in exploiters are depicted in figure 5. As a point of reference, the conventional exploiter isocline is depicted as a dashed line. The horizontal distance between the conventional isocline and the one for time-delayed numerical response can be interpreted as the numerical change that the victim population undergoes during the lag period of the exploiter.

The isocline for exploiters with time-delayed numerical response does not even qualitatively resemble the rightward-tilted exploiter isoclines of ratio-dependent models (fig. 3). Instead of having a positive slope and starting from the origin, the exploiter isocline has a negative slope and meets the victim axis further from the origin than is the case with the conventional model. Moreover, the equilibrium is exactly the same as in conventional victim-dependent models. Thus, the system will also respond to enrichment just as the conventional one. When the victim isocline expands because of increased productivity, the equilibrium point will climb along the dashed isocline. The course of the solid exploiter isocline depends on the shape of the prey isocline: it will always cross the dashed exploiter isocline at the equilibrium point. Consequently, it is inadmissible to use the same solid exploiter isocline for systems with different primary productivities.

Basically the same thing happens when considerations on feeding history are applied to three-dimensional exploitation models. The leftmost part of the prey (herbivore) isocline, which is vertical in the model of Oksanen et al. (1981, fig. 2), obtains a negative slope. The carnivore isocline bends along its line of intersection with the herbivore isocline in a way that is difficult to communicate graphically. However, whether the system is two or three dimensional, it is still true that feeding history cannot possibly influence the location of the equilibrium point, because at equilibrium, past conditions are identical with present ones.

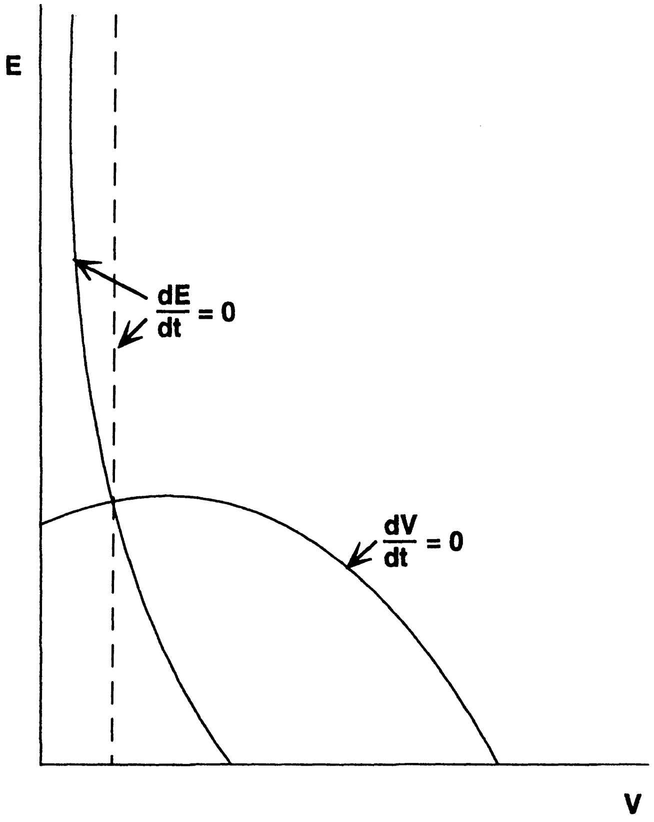

FIG. 5.—A graphical exploiter-victim model (*E*, exploiter; *V*, victim) with time-delayed numerical response of exploiters. The exploiter isocline for a corresponding system with immediate numerical response is depicted as a *dashed line*.

Consequently, the response of a laissez-faire exploitation system to increasing primary productivity will correspond to the predictions of Oksanen et al. (1981).

The main change caused by time-delayed numerical response is reduction in the local stability of the exploiter-victim equilibrium. The existing body of stability theory tells that exploiter-victim systems tend to be stabilized by a negative slope of the victim isocline and by a positive slope of the exploiter isocline (Rosenzweig and MacArthur 1963; Rosenzweig 1971, 1973, 1977; Tanner 1975). The negative slope of the exploiter isocline is thus destabilizing, which conforms to the general theory of the impact of time delays on population dynamics (May 1981).

Indeed, interference competition, territoriality, and spatial heterogeneity may straighten up the exploiter isocline and tilt it rightward even in systems with time-delayed numerical response in predators, thus enhancing stability and leading to a situation in which enrichment results in higher equilibrium densities in both exploiters and victims (Rosenzweig and MacArthur 1963; Beddington 1975;

Murdoch and Oaten 1975; Tanner 1975; Hassell 1981). In that case, the positive slope exists in spite of the impact of the slow population-dynamical time scale, not because of it.

AN ISOCLINE APPROACH TO DISCRETE-TIME EXPLOITER-VICTIM SYSTEMS

Another interpretation of the Arditi-Ginzburg argument is that they intended to develop an isocline model of discrete-time exploiter-victim systems with strictly seasonal reproduction in both expoiters and victims. Such discrete-time exploiter-victim models are commonplace in studies dealing with arthropod hosts and their parasitoids (e.g., Hassell 1981; Kareiva 1984). However, the isocline technique is not normally used in this context, and for good reason. The technique is based on the theory of differential equations. When studying net changes over a time period with positive duration (i.e., not instantaneous changes), we enter the world of difference equations in which the terms of analysis are entirely different.

Of course, zero isoclines can be defined for net annual changes too. We can define $\Delta V/\Delta t$ as the net annual change in victim density and $\Delta E/\Delta t$ as the net annual change in exploiter density, and there will be some density combinations for which $\Delta V/\Delta t = 0$, and other combinations satisfying the condition $\Delta E/\Delta t = 0$. However, these combinations depend on the point of the annual cycle to be considered. Moreover, they cannot be directly deduced from standard exploiter-victim equations, because functional response cannot be defined in the context of net changes over a long time. (Functional response is defined as the number of prey killed per predator per unit of time for a fixed prey density and thus only exists in the context of instantaneous dynamics.) The isoclines can be solved by treating reproduction and mortality separately and by breaking Δt down into short intervals (e.g., days), within which the instantaneous approach passes as a fair approximation. Net annual changes can then be solved by means of iteration.

We will restrict our simulations to the case in which exploiters are carnivores and victims are herbivores. Consequently, exploiters will be called predators and victims will be called prey. Moreover, we assume that the plants have subterranean energy resources that are inaccessible for grazers when the ground is frozen. Consequently, it can be assumed that the production of shoots in the spring does not depend on the remaining shoot biomass in the spring. The dynamics of the system can then be studied by means of two-dimensional exploitation models in which the impact of grazers on plants is only implicitly included as a source of density-dependent winter mortality (cf. Oksanen 1990*a*). We admit that this simplification decreases the generality of our results. There are many seasonal systems in which forage production does depend on remaining biomass (e.g., reindeer feeding on lichens, lemmings feeding on mosses). Such systems need to be analyzed by means of three-dimensional discrete-time models.

Using the iteration approach above, we have made a large number of simulations, which allowed us to map predator and prey isoclines with a fair amount of confidence, to study the dynamic behavior of the system and to study its response to enrichment. The details of the simulation are explained in the Appendix. The basic features are as follows: (1) Plant and animal production occurs seasonally.

After the spring flush, plant biomass is gradually depleted by grazers and restored next spring to its previous level. (2) The herbivorous prey animals are assumed to reproduce at their maximal rate, unless the number of reproducing females becomes limited by shortage of territories. (3) In the absence of predation, herbivores maintain high survival rates, unless plant biomass is depleted to very low values, at which survival rates rapidly decline. (4) Predators reproduce when prey densities are above a certain threshold (which can be zero but was usually assumed to be positive). (5) Predators have high survival rates until prey densities are reduced below a threshold value, at which survival rates of predators rapidly decline. (6) Except for the seasonal reproduction, daily dynamics of predation conform to equations (1) and (2).

The isoclines thus produced are depicted in figure 6*A*. The prey isoclines have a steep, almost vertical part at very low prey densities. This "technical refugium" at low densities exists, because predators then quickly die or emigrate. Next, the prey isocline has a section with positive slope, because of predator saturation. The positive segment continues until either social regulation starts to slow the per capita prey reproduction or until winter resources become limiting for the prey. Where social interactions begin to limit the number of reproducing females, the prey isocline is tilted to less positive or even negative slopes depending on clutch sizes and survival. At prey densities at which winter resources become limiting, the annual net change in prey numbers always becomes negative. Within this range of prey densities, moderate predator numbers improve net winter survival of the prey by preventing overexploitation of winter resources. Consequently, the right-hand side of prey isocline looks like an overhanging cliff, making the overall shape of the isocline highly unusual.

Assuming a positive threshold prey density for predator reproduction, the predator isocline has a vertical section below the prey isocline (fig. 6*A*). In cases in which predators are assumed to reproduce regardless of prey density (fig. 6*B*), the predator isocline retains a positive slope even below the prey isocline, because the postreproductive survival rate of predators is then very sensitive to the rate of increase of prey numbers, and this rate depends on predator density. In this special case, the predator isocline can meet the prey axis close to the origin. Consequently, the predator isocline has similarities with the one generated by the ratio-dependent model of Arditi and Ginzburg (1989). Above the prey isocline, numbers of prey decrease; the more predators, the more rapid the decrease. Thus, the predator isocline is always tilted rightward in this part of the phase space.

Enrichment only influences the position of the overhanging part of the prey isoclines. In relatively unproductive systems, the overhang meets the upward-sloping part of the prey isocline. In extremely barren ecosystems (not depicted in fig. 6*A*), this meeting may take place on the left-hand side of the vertical section of the predator isocline. In this case, a predator-prey equilibrium does not exist even theoretically. However, even if the isoclines intersect, because of somewhat higher levels of enrichment (fig. 6*A*, prey isocline labeled "low") or because of a strongly tilted predator isocline (fig. 6*B*), the system is always both locally and globally unstable. Prey populations explode and crash, because of overexploita-

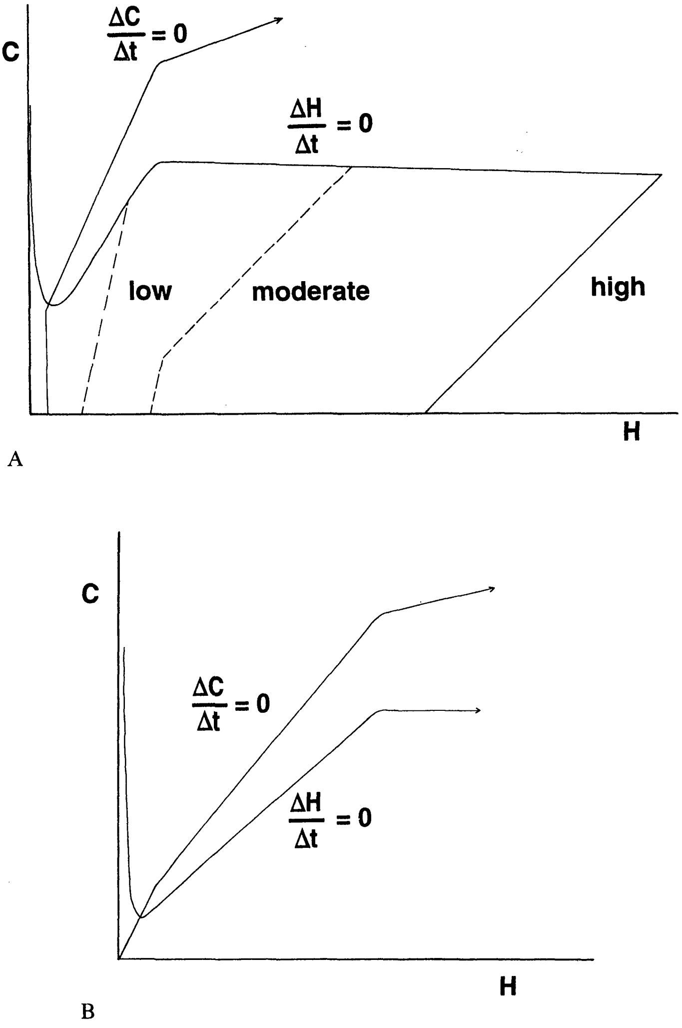

FIG. 6.—A discrete-time exploiter-victim isocline model (*C*, predator; *H*, prey). Isoclines refer to density combinations for which the annual net change of exploiters and victims is zero. *High, moderate,* and *low* denote plant productions of 16×10^6, 8×10^6, and 4×10^6 units per unit area, respectively. *A*, Threshold of 100 prey for predator reproduction; *B*, no threshold for predator reproduction.

tion of winter resources, and the predators consequently die from starvation. The system thus cannot sustain predators and is better analyzed through herbivore-plant models as done by Oksanen (1990*a*) for seasonal herbivore-plant systems. When the overhang lies so far to the right that a substantial part of the prey isocline has negative or zero slope, predation will be more important than starvation, thus making sustained carnivore-herbivore cycles possible (fig. 7). Under

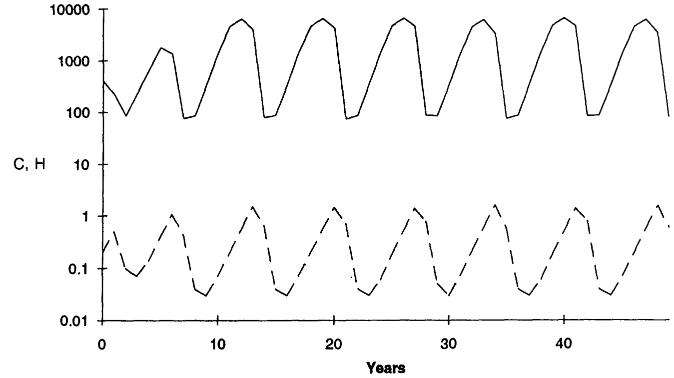

FIG. 7.—Population dynamics of predators (*C*, *dashed lines*) and prey (*H*, *solid*) in a productive environment in which the predators have alternative resources. See Appendix for details.

such circumstances, introducing switching behavior of the predators (to alternate prey or inactivity) at very low prey densities into the model (see Appendix) seems sufficient to cause sustained cycles. Once the primary productivity of the system is sufficient for sustained predator-prey cycles, further enrichment has no impact on the population dynamics.

The failure of the system to respond to further enrichment has a simple biological background. In strongly seasonal systems, the spring flush will produce enough food for herbivore reproduction. Enrichment only determines whether food will run out before the next spring, in which case the system collapses, or whether food will last, in which case the dynamics of the system will depend on other factors (social regulation in herbivores, carnivore-herbivore interactions). The results thus suggest that the dichotomy between the self-regulatory view of Chitty (1960) and Krebs and Myers (1974), for example, and the predation-centered view of Hairston et al. (1960), Fretwell (1977), and Oksanen et al. (1981) may be somewhat artificial. In addition to a sufficient level of enrichment, social regulation is essential for preventing an outbreak followed by a collapse. Predation, in turn, acts as the proximate cause initiating and sustaining population declines that are difficult to understand on the basis of processes within a single population (Stenseth 1986).

In spite of some similarities between our isoclines and those of Arditi and Ginzburg (1989), our conclusions on dynamics and responses to enrichment are totally different. According to their predictions, enrichment leads to increased densities of both predators and prey, whereas we predict that over a wide range of productivities neither predators nor prey respond to enrichment. Moreover, both populations are predicted to undergo violent cyclic fluctuations in cases in which peaks in prey (herbivore) densities depend on their social system, whereas their rock-bottom levels depend on the availability of alternative food sources for predators and on the prey density at which doing nothing becomes a better choice for predators than desperate hunting.

PREDICTIONS AND DATA ON PLANTS

The two classes of models generate radically different predictions on the relationship between plant biomass and primary productivity. According to ratio-dependent models, the relation should be linear and the regression line should point toward the origin (see fig. 4). Conversely, victim-dependent models without interference competition predict that there is no relation whatever between aboveground plant biomass and primary productivity in relatively barren areas. There should then be a productivity threshold at which the relation is positive and almost linear, provided that other factors (e.g., geographical isolation) do not prevent carnivores from invading the system (fig. 2). On the basis of a limited number of data points Oksanen et al. (1981) proposed that the threshold lies at the productivity of about 700 g $m^{-2}yr^{-1}$ (dry wt).

The prediction was tested by Oksanen (1983) after the publication of a new data set from the Arctic (the results of the American-IBP project at Barrow, Alaska). Although the results were supportive to the model of Oksanen et al. (1981), the test had a clear shortcoming. The material only included three data points above the 700 g $m^{-2}yr^{-1}$ threshold. Thus, the change in the relationship between aboveground plant biomass and primary productivity at this threshold was not adequately documented.

The reason for the poor representation of more productive communities in the material was that the coniferous forest IBP projects focused on the production of trees and did not yield estimates of total primary productivity. However, productivity estimates in which the field layer is included have now been shown to us. These include pine and birch forests in southern Finland (Mälkönen 1974, 1977), south Finnish drained bogs (Paavilainen 1980), and a mesic spruce forest in northern Sweden (Albrektson and Lundmark 1991). The main problem with these data is that gross productivity has not been estimated and the net production of trees is highly sensitive to the developmental stage of the stand (Ilvessalo 1952). The percentage of heterotrophic tissues is essentially higher in trees than in herbaceous plants and dwarf shrubs. Even when growing at their best, about 50% of the gross primary production of trees goes to respiration or is allocated to mycorrhizal fungi, and in mature forests this percentage is still much higher (Kira and Shidei 1967; M. Hagner, personal communication). In gradients from tundra to taiga, the relation between aboveground biomass and primary productivity may thus seem to change just because the productivity estimates for the taiga are biased. To avoid such fortuitous corroborations, we have multiplied the productivity estimates for scrubs (height <2 m) by 1.25, those for low woodlands (2 m < h < 10 m) by 1.5, and those for genuine forests (h >10 m) by 2. The primeval taiga was excluded from the analysis. Because of the rather arbitrary nature of these correction coefficients, we also present the uncorrected data. From the Arctic, we include those data points that represent widespread habitats typical for the zone in question, but we exclude the isolated sedge-moss communities of Devon Island, where the key grazer of these habitats (the brown lemming, *Lemmus sibiricus*) is missing.

The results (fig. 8) show that the pattern does indeed change at the transition

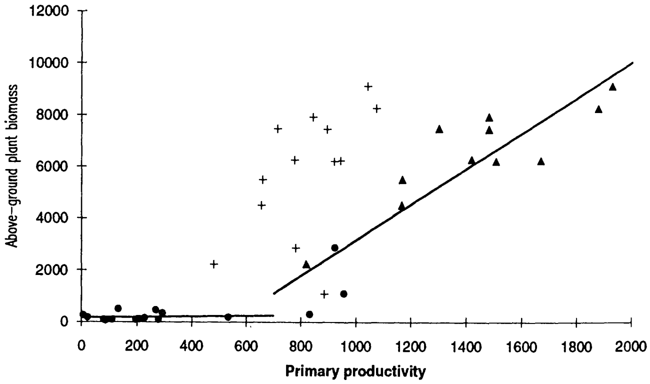

FIG. 8.—The relationship between annual net aboveground productivity (NAP; g $m^{-2}yr^{-1}$) and aboveground plant biomass (B; g m^{-2}). The line below 700 g $m^{-2}yr^{-1}$ is the regression $B = 0.12$ (NAP) $+ 168.4$, $p = .71$, $r^2 = 0.01$, and the line above 700 g $m^{-2}yr^{-1}$ is the regression $B = 6.87$ (NAP) $- 3{,}705.0$, $p < .0001$, $r^2 = 0.81$. *Filled circles* are arctic and subarctic data points, *pluses* are uncorrected boreal data points, and *filled triangles* are the corrected boreal and subarctic data points.

from typical tundra to subarctic and boreal vegetation. Below the 700 g $m^{-2}yr^{-1}$ threshold, there is hardly any indication of a positive relationship between primary productivity and aboveground plant biomass. The slope of the regression line (0.12) is not significantly different from zero ($r^2 = 0.01$, $p = .71$). The three data points with high phytomass values represent a bog, dominated by relatively inedible *Sphagnum* mosses, a lichen heath in an area in which the wild reindeer are managed to prevent overgrazing (see Gaare and Skogland 1975), and a polygon center community in which snow conditions are maximally unfavorable for lemmings. Thus, rather than reflect primary productivity, variation in aboveground plant biomass seems to reflect human impacts on grazers and differences in edibility and in grazing conditions.

Conversely, above the threshold, the slope is significantly positive and steep (6.87) and the statistical significance of the relation is beyond reasonable doubt ($r^2 = 0.81$, $p < .0001$). The corrected data imply that a moist and nutrient-rich south boreal site is about twice as productive as a low-arctic willow scrubland on Hardangervidda. The mean July temperature on Hardangervidda was 7.4°C (Sonesson et al. 1975), 10°C lower than in southern Finland, where the growing season starts in early May, which is 1 mo earlier than on Hardangervidda. The twofold difference between primary productivity of moist and nutrient-rich sites implied by figure 8 is more consistent with these differences in abiotic conditions than the modest productivity difference implied by uncorrected data. Notice that the main impact of the correction coefficient is to change the slope of the regression, whereas impact on statistical significance is marginal.

A thinkable trivial explanation for the difference could be that substantial biomass accumulation is only possible in communities dominated by woody plants.

This is not true. On the high-arctic Devon Island where brown lemmings do not occur, there is a steep, positive relationship between primary productivity and aboveground plant biomass (Oksanen 1983). The highest values (1.3 kg m^{-2}; Bliss 1977) are comparable with those of the low-arctic willow thickets in spite of the absence of woody plants. On the totally grazer-free Signy Island in the Antarctic, aboveground plant biomass ranges from 2 to 10 kg m^{-2} (Collins et al. 1975), corresponding to the range of the boreal forest sites in figure 8.

Two-link ecosystems with essentially higher primary productivity than tundra areas constitute especially instructive case points. Such a situation prevails on the atoll of Aldabra in the Indian Ocean, where the herbivorous giant tortoises lack significant predators. The grazer biomass is 350 kg ha^{-1}, which by a wide margin surpasses long-term values reported from other natural ecosystems (Coe et al. 1976). Thus, the island must be relatively productive. Yet, the natural inland vegetation consists of closely clipped "tortoise turf" that seldom exceeds 5 mm in height (Hnatiuk et al. 1976; Merton et al. 1976). We are unaware of reports of plant biomass from typical "tortoise turf" communities of inland areas. However, aboveground biomass from grazed coastal *Sporobolus virginicus* stands was reported by Hnatiuk et al. (1976) to be only 104 g m^{-2}. This is in the low part of the range of aboveground biomass in tundra and steppe communities. The giant tortoises cannot survive without shade, and they cannot move in rough terrain that limits their distribution on the island. The lawnlike communities occur only in grazed areas, whereas ungrazed parts of the atoll support several times higher plant biomass and an entirely different kind of vegetation (Hnatiuk et al. 1976; Merton et al. 1976). There can thus be no doubt about the causal connection between grazing and the low aboveground biomass of grazed areas.

Another corresponding case is the sub-Antarctic island South Georgia, where the introduced reindeer populations have increased strongly since the end of the 1950s (Leader-Williams 1988). In spite of the relatively frigid climate, coastal grasslands of South Georgia are extremely productive (annual dry-matter production about 6 kg m^{-2}) and, in an ungrazed state, also support copious aboveground biomass (about 7.5 kg m^{-2}; see Smith and Walton 1975). Today, plant biomass in large parts of the coastal grasslands has dramatically declined. As the original plant cover remains intact in areas not accessible to reindeer and can be quickly restored in exclosures (Leader-Williams 1988), we can rule out the possibility that the vegetational changes were due to climatic factors. Although we are not aware of any biomass data from grazed areas, we suggest (J. Moen, personal observations) that the grazed meadows have similar aboveground biomass as typical tundra ecosystems.

The same rule seems to apply to rivers (Power 1984, 1990; Power et al. 1985), ponds (Ranta et al. 1987), lakes (Levitan et al. 1985), maritime intertidal habitats (Lubchenco and Gaines 1981), and benthic ones (Simenstad et al. 1978). Systems with herbivores but without significant carnivores have consistently very low biomass of edible algae, no matter how productive they are. In systems with large-bodied herbivorous fishes, all algae are edible, and abundances of all macroalgae are very low.

PREDICTIONS AND DATA ON HERBIVORES

The diagnostic predictions on herbivore biomass refer to relatively productive ecosystems. All models predict that herbivore biomass responds positively to increased primary productivity in relatively barren steppe and tundra ecosystems. The Arditi-Ginzburg model of ratio-dependent predation predicts that the same relation also holds for more productive ecosystems (fig. 4). According to the most simple variant of victim-dependent models (Oksanen et al. 1981), the trend should totally level off at the productivity threshold of 700 g $m^{-2}yr^{-1}$ (fig. 2). Models with substantial interference between carnivores (e.g., Wollkind 1976) predict that a positive relation exists even in more productive ecosystems but with a substantially lower slope. The same prediction is generated by the model of Oksanen (1992), which includes the evolutionary and behavioral responses of herbivores to predation.

McNaughton et al.'s (1989, 1991) review of global biomass patterns in herbivores supports the predictions of the ratio-dependent model. However, they only tested for a log-linear pattern in the data. A reanalysis using a model with built-in leveling off of the herbivore biomass at high values of primary productivity gave an equally good fit to the data (Moen and Oksanen 1991). Moreover, when separate regressions were made on each side of the 700-g $m^{-2}yr^{-1}$ threshold predicted by Oksanen et al. (1981), a significantly lower slope was found in the high-productive end of the gradient. An attempt to reexamine the data sources of McNaughton et al. (1989, 1991) gave the same general patterns, but it also highlighted the extremely mixed quality of the data (Moen and Oksanen 1991).

The materials of McNaughton et al. (1989, 1991) and Moen and Oksanen (1991) contained many data points for which the assumption of undisturbed trophic dynamics is highly dubious. In most temperate and boreal areas, ungulates are game animals and their numbers are determined by hunting policies, not by natural consumer-resource dynamics. Only in arctic and tropical zones and in deserts is it easy to find areas that can be assumed to satisfy the criterion that trophic dynamics are reasonably uninfluenced by man. In the humid and semiarid parts of boreal and temperate zones, this criterion may be satisfied in large national parks and in some especially remote areas, but we are unaware of relevant data from such systems. Thus, we restricted our data base to arctic and tropical areas and to deserts, and even there we rejected areas with obvious and heavy human interference.

An additional problem is provided by the fact that herbivore biomass and primary productivity are rarely measured from the same habitat. McNaughton et al. (1989, 1991) and Moen and Oksanen (1991) accepted precipitation-based productivity estimates from tropical grasslands that ignore, for example, the impact of bedrock on the availability of nutrients and is based on regression lines that are debatable even as generalizations (Rutherford 1980). We chose a somewhat more conservative approach and only accept direct measurements. However, to retain a reasonable number of data points, we do not require that the measurements of primary productivity and herbivore biomass were from the same spot; it is

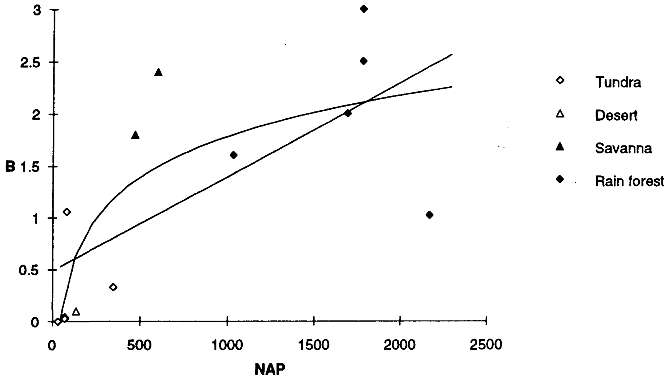

FIG. 9.—The relationship between annual net aboveground productivity (NAP; g $m^{-2}yr^{-1}$) and herbivore biomass (B; g m^{-2}). The *straight line* is the regression $B = 0.0009$ (NAP) + 0.49, $p = .01$, $r^2 = 0.47$, and the *curved line* is the regression $B = 1.30 \log(\mathrm{NAP}) - 2.12$, $p = .001$, $r^2 = 0.62$.

deemed sufficient if the data points are from the same region and from areas with similar climate and geology.

With these criteria, we obtain 14 data points: five from tundra areas (Wielgolaski 1975*b;* Bliss 1977; Batzli et al. 1980), three from tropical grasslands (Sinclair 1975; Bunderson 1986), five from tropical forests (Odum 1970; Jordan 1983; Owen 1983; Prins and Reitsma 1989), and one from a temperate desert (Chew and Chew 1970; see fig. 9). Two data points (Hardangervidda and Barrow) represent cases in which herbivore biomass was not averaged over time. However, available information was sufficient for computing average grazer biomass (Wielgolaski 1975*b;* Batzli et al. 1980). Two of the data points represent winter (Truelove Lowland) or dry season (Tarangire, Tanzania) concentration areas for key herbivores. The case of Truelove Lowland could be solved, because the regional average of musk-oxen densities for corresponding areas of northeastern Devon Island was reported (Hubert 1977). The number of musk-oxen days in Truelove Lowland was 2.5 times the regional average. Thus, musk-oxen biomass of Truelove Lowland was multiplied by 0.4. In the case of Tarangire, there was no quantitative information allowing corresponding computations. Thus, the data point was excluded from the analysis. (With its extremely high grazer biomass [$B = 10.1$ g m^{-2}] and relatively low productivity [net aboveground primary productivity (NAP) = 325 g $m^{-2}yr^{-1}$] it was a true outlier, whose retention would have made all relations nonsignificant.)

Because of the low number of data points, we restricted our analysis to the question whether the logarithmic model with built-in leveling off of the trend ($B = a \log(\mathrm{NAP}) + b$) works better than the linear one ($B = a(\mathrm{NAP}) + b$, where a and b are constants to be estimated from data). To be conservative, we do not correct the estimates of tree production. Thus, the test is biased in favor of the ratio-dependent model.

Both the linear model and the logarithmic one yield a statistically significant positive correlation. However, the logarithmic model ($r^2 = 0.62$, $p = .001$) performs clearly better than the linear one ($r^2 = 0.47$, $p = .01$). Notice also that the slope of the logarithmic relation declines most rapidly at NAP values of about 250 g $\mathrm{m}^{-2}\mathrm{yr}^{-1}$. With a shoot : root allocation ratio of 1 : 3, this corresponds roughly to the total productivity threshold of 700 g $\mathrm{m}^{-2}\mathrm{yr}^{-1}$ proposed by Oksanen et al. (1981) for tundra areas. This shoot:root ratio seems to be representative for nonwoody vegetation in typical tundra areas in Scandinavia and North America (Wielgolaski 1975*a;* Muc 1977; Miller et al. 1980). Notice that the uncorrected productivity estimates for tropical rain forests are only marginally higher than corresponding values for boreal forests with a cool and short growing season. It is thus probable that the data on the actual production of mature rain forests grossly underestimate their potential productivity and that the leveling off of B is thus much stronger than indicated in figure 9.

Moreover, our arctic grazer data are likely to be below the truly natural equilibrium level. The impact of management on the wild reindeer of Hardangervidda has already been mentioned, but sustained human impacts also extend to the Arctic proper. Still two decades ago, both musk-oxen and caribou populations of the American Arctic were under the threat of extinction because of excessive hunting with firearms (Tener 1965; Kelsall 1968). The IBP studies were performed only 10–15 yr later. The musk-oxen population of northeastern Devon Island increased by 65% between 1964 and early 1970s (Hubert 1977), and also the caribou populations of arctic Alaska seem to be increasing (Batzli et al. 1980). Thus, it would be useful to repeat IBP-type studies in the Arctic now that the restoration of natural dynamics has proceeded further. Corresponding studies in undisturbed tropical ecosystems and in relatively large boreal and temperate national parks would also be useful.

Before such studies have been conducted, definite conclusions on the relation between herbivore dynamics and primary productivity are not warranted. However, available data are more compatible with the predictions of the victim-dependent models than with those of the ratio-dependent ones.

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APPENDIX

THE SIMULATION IN DETAIL

The basic feature of the model is to divide the year into two discrete periods: a reproductive period during which the populations increase and a nonreproductive period during which the populations decrease. The reproductive period is concentrated into 1 d, which, although unrealistic, is not critical for the qualitative results. Assuming a longer reproductive period would mostly change the quantitative results.

Isoclines were iterated from simulations over 1 yr starting just before the reproductive period. As a model system we used a lynx-hare system, but isocline behavior for parameters with more extreme values was also studied (the studied parameter range is denoted in parentheses after each parameter). Plants are included only as food source for herbivores and the model does not include plant population dynamics. Plants are thus included as biomass rather than as populations. The annual production of aboveground biomass depends only on the productivity of the habitat.

THE REPRODUCTIVE PERIOD

The reproduction of plants, herbivores, and carnivores are included in the model with the following equations:

$$\frac{\Delta P}{\Delta t} = k, \tag{A1}$$

$$\frac{\Delta H}{\Delta t} = \begin{cases} r_h H & \text{if } H < 2T & \text{(A2)} \\ r_h 2T & \text{if } H \geq 2T, & \text{(A3)} \end{cases}$$

and

$$\frac{\Delta C}{\Delta t} = \begin{cases} 0 & \text{if } H < H_c & \text{(A4)} \\ r_c\{1 - e^{-[h(H-H_c)]}\}C & \text{if } H \geq H_c, & \text{(A5)} \end{cases}$$

where P, H, and C are population densities of plants, herbivores, and carnivores, respectively, k is a constant describing annual plant biomass increase ($2 \times 10^6 < k < 16 \times 10^6$ − biomass units/unit area), r_h and r_c are the maximum numbers of yearly offspring per reproducing individual of herbivores and carnivores, respectively ($1 < r_h < 9$; $1 < r_c < 3$), T is the maximum number of reproducing females ($T = 500$), H_c is the herbivore density below which carnivores will not reproduce ($0 < H_c < 100$), and h is a constant that is fitted to describe how fast maximum reproduction is reached ($0.1 < h < 0.007$). The greater h, the faster maximum reproduction is achieved.

THE NONREPRODUCTIVE PERIOD

Mortality and biomass depletion were included in the model in the form of the following equations:

$$\frac{\Delta P}{\Delta t} = -\frac{W_h}{D_h + P}HP, \tag{A6}$$

$$\frac{\Delta H}{\Delta t} = -\frac{W_c}{D_c + H}HC - Hm_h(e^{-\beta P}), \tag{A7}$$

and

$$\frac{\Delta C}{\Delta t} = \min \begin{cases} -m_{\min} & \text{(A8)} \\ -m_c C + q\frac{W_c}{D_c + H}HC, & \text{(A9)} \end{cases}$$

where $W_h P/(D_h + P)$ and $W_c H/(D_c + H)$ is the functional response (Type II sensu Holling 1959), W_i is the foraging rate of saturated consumers and D_i is the half-saturation constant of herbivores and predators, respectively ($2.5 < W_h < 5$, $D_h = 2{,}000$, $2.5 < W_c < 7.5$, $100 < D_c < 200$), m_h and m_c are the mortality rate of starving herbivores and carnivores, respectively ($m_h = m_c = 0.1$). For herbivores, the mortality was assumed to decrease exponentially with increasing food abundance. (The use of equations explicitly based on feeding and maintenance yielded practically identical results.) The constant β describes how fast mortality declines with increasing abundance of food (β was chosen such that $e^{-\beta P} = 0.5$ for $P = 2{,}000$; $\beta = 0.0003$), $m_{\min}$ is the carnivore mortality in cases in which food is not limiting ($m_{\min} = 0.001$), and q is the conversion efficiency of captured prey to energy for maintenance. The impact of food shortage on carnivore mortality was modeled after the standard predator equation (A9). The second term is thus the numerical response, including both mortality and reproduction. As carnivores are not assumed to reproduce during this period, their mortality changes to equation (A8) as they energetically break even. The energetic threshold corresponds to the reproductive threshold, and q was chosen such that equation (A9) $= 0$ at $H = H_c$.

Changing W_c, D_c or q, or r_h or r_c will change the inclination of herbivore and carnivore isoclines as well as their quantitative place in the phase space. This will not move the inflection point in the predator isocline below the prey isocline as both isoclines change simultaneously. Changing the constants of $[W_h/(D_h + P)]$ or $[m_h(e^{-\beta P})]$ has the same effects as changing biomass production (cf. fig. 6).

PREDATOR SWITCHING

Switching behavior of the predators was introduced in the model by the following condition:

$$\frac{\Delta C}{\Delta t} = \begin{cases} -m_s & \text{if } H < H_s \\ \min\begin{cases} -m_{\min} \\ -m_c C + q\dfrac{W_c}{D_c + H}HC \end{cases} & \text{if } H > H_s, \end{cases} \tag{A10}$$

where m_s is the maximum mortality of carnivores when the alternative prey was present ($m_s = 0.01$), and H_s is the density of herbivores when switching occurred ($H_s = 85$). The isoclines are not affected by this except for the left, almost vertical part of the prey isocline, which becomes more or less absolutely vertical (at $H \approx 86$).

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