

Coupling in Predator–Prey Dynamics: Ratio-Dependence

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In continuous-time predator–prey models, the *per capita* rate of consumption (the functional response or “trophic function”) is usually interpreted as a behavioral phenomenon. The classical assumptions are that predators encounter prey at random and that the trophic function depends on prey abundance only. We argue that this approach is not always appropriate. The trophic function must be considered on the slow time scale of population dynamics at which the models operate—not on the fast behavioral time scale. We propose that, in cases where these two time scales differ, it is reasonable to assume that the trophic function depends on the *ratio* of prey to predator abundances. Several field and laboratory observations support this hypothesis. We compare the consequences of the two types of dependence with respect to the dynamical properties of the models and the responses of population equilibria to variations in primary production. In traditional prey-dependent models, only the predator population responds to primary production, while both levels respond in ratio-dependent models. This result is generalized to food chains. We suggest that the ratio-dependent form of the trophic function is a simple way of accounting for many types of heterogeneity that occur in large scale natural systems, while the prey-dependent form may be more appropriate for homogeneous systems like chemostats.

Introduction

In predation theory, differential equations are used in cases where it can be assumed that generations overlap and that populations vary continuously in time. For this approach to be reasonable, the time scale must be chosen in a way appropriate to the organisms under study. For most mammals, for example, variation should be described on a yearly time scale; for many planktonic organisms, a daily scale is required. In cases where population dynamics cannot be approximated by continuous functions, difference equations may be more appropriate. The Lotka–Volterra model with which predation theory originated has many shortcomings that are widely recognized. Nevertheless, the use of differential equations has remained an invaluable tool in subsequent elaboration of the theory, and this approach permeates much of current ecological thinking.

The consumption rate of a single predator (its “functional response” g) is a key component of predation models since it is considered to determine both the prey death rate and the predator rate of increase (usually modeled as proportional to the rate of feeding). For this reason, it might better be called the “trophic function”

(Svirezhev & Logofet, 1983, p. 80). A common assumption is that this function is determined by prey abundance N as the only variable:

$$g = g(N). \quad (1)$$

This assumption was used in the Lotka-Volterra theory as well as in the other seminal studies of predator-prey systems (Holling, 1959a; Rosenzweig & MacArthur, 1963; Rosenzweig, 1971; May, 1973), and it is still not questioned in recent monographs dealing with the subject (Taylor, 1984; Curry & Feldman, 1987).

Any dependence on predator abundance P is neglected on the strength of an analogy to the "law of mass action" in chemistry. The initial idea is that, like an agitated solution of reacting molecules, predators and prey encounter each other randomly, the number of encounters per predator being proportional to prey density (e.g. Royama, 1971). Bacteria feeding in a stirred chemostat can be viewed as a good biological exemplification of this model. Deviations from this simple proportional relationship are attributed to additional complexities in patterns of behavior. For example, prey handling time leads to the well known "disk equation" (Holling, 1959b) and to its generalization for parasitoids (Arditi, 1983); sigmoid responses are generated by prey switching (Murdoch & Oaten, 1975) or by density-dependent searching efficiency (Hassell *et al.*, 1977). This behavioral approach underlies most of the theoretical and experimental work on the functional response (review by Hassell, 1978). In this approach, it has been pointed out that interference competition between individual predators will be a source of predator-dependence in g , which must decline with P (Beddington, 1975; DeAngelis *et al.*, 1975; Kuno, 1987). Estimates of mutual interference for arthropods in field and laboratory conditions show that this effect cannot be neglected (Hassell, 1978).

In our view, the foregoing behavioral arguments are not sufficient for constructing models of population dynamics because they must operate on a generation time scale much longer than the behavioral time scale. In such cases, the trophic function must be calculated on the same time scale as reproduction and mortality, and it may be completely different from the behavioral response. Overlooking the importance of spatial and temporal scales, Wiens *et al.* (1986) have shown how changing scales can yield different answers to the same question. Taking their example of coyotes and jackrabbits, eqn (1) means that the number of rabbits consumed per coyote in a unit of time would remain unchanged if the coyote population were doubled. On a daily time scale, the individual feeding rate can probably be modeled as the result of random encounters between prey and predators hunting independently from one another. 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*:

$$g = g\left(\frac{N}{P}\right). \quad (2)$$

The rationale behind the exclusion of predator-dependence in eqn (1) was made explicit by Rosenzweig & MacArthur (1963). In recognition of the fact that predator density is expected to adversely affect the number of predators being produced, the authors stated: "... the greater the number of predators, the faster the [prey] density is reduced; still the instantaneous rate of change of the predator population depends only on the instantaneous rate of kill, which depends on the instantaneous density of prey." Restating the same idea, Rosenzweig (1977) explained that the effect of predator density on predator growth passes through prey dynamics. This argument holds well if all "instantaneous" values refer to variables varying on the same time scale—if an instant of feeding is of the same order of magnitude as an instant of reproduction/mortality. This will only be the case in homogeneous systems with high turnovers, comparable to chemostats. Significantly, all examples given by Rosenzweig (1977) are from microbial or planktonic systems.

In more general situations, the time scales of feeding and reproduction/mortality will be different and the trophic function must account in a simple "macroscopic" way for the intricacies of the predation process. Because of the spatial and temporal heterogeneities that are present on the "microscopic" scale, various phenomena will induce predator-dependence in the feeding rate when calculated on the generation scale, even if predators do not interfere directly. This can arise, for example, because of predator aggregation in patches and local prey extinctions. This "pseudo-interference" has been clearly demonstrated in many detailed models of host-parasitoid interaction (e.g. Free *et al.*, 1977). Other types of heterogeneities, like intermittent prey reproduction, will have similar effects. When described in continuous time, that is, when viewed on large spatial and temporal scales, predators will appear to *share* food as a result of the cumulated effects of such heterogeneities, in addition to direct interference.

In general, a predator-dependent trophic function will be of the form $g = g(N, P)$. The specific ratio-dependent form (2) is the extreme case of "perfect sharing", as the prey-dependent form (1) is the extreme case of "non-sharing". The purpose of the present paper is to determine which of the ends of this spectrum better describes general predator-prey systems:

$$g(N) \leftarrow g(N, P) \rightarrow g\left(\frac{N}{P}\right).$$

It is of great interest to be able to model predation with a simple expression. It is needed, for example, in theoretical studies of general ecosystem properties, like food web dynamics. In such studies, authors usually retreat to predator independence (1), often in the form of the Lotka-Volterra expression $g(N) = \alpha N$ (e.g. Pimm, 1982). We propose that, as an alternative, eqn (2) can be used as a simple description of sharing effects, with no necessity of modeling individual predator behavior or individual prey patches. We expect the function $g(N/P)$ to be of the general shape indicated on Fig. 1. With the ratio as abscissa, the *per capita* consumption rate first increases linearly for low ratios of abundances, $g \propto N/P$, but it is then limited by some upper value when food is superabundant. Getz (1984) has shown how a

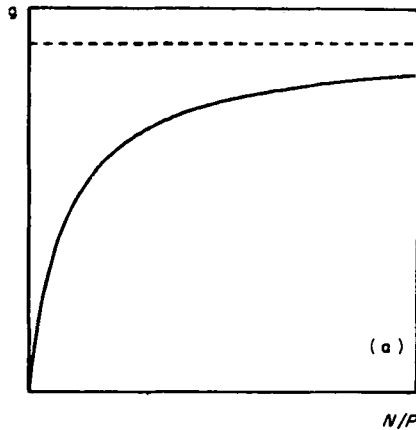


FIG. 1. The *per capita* rate of consumption is expected to be concave and monotonic, characterized by an initial slope α and an upper asymptote.

ratio-dependent approach can provide a unified structure for modeling the dynamics of a single population, of predation, and of competition.

As the law of mass action is the idealization of prey-dependence, an idealized mechanism that would induce ratio-dependence is the following. Let the time scale of population dynamics be much slower than the time scale of feeding. When viewed from the slow time scale, prey abundance is assumed to appear as a continuous function. However, when viewed from the fast behavioral time scale, prey production is no longer continuous but appears as successive "bursts". Between these bursts, the predators consume the prey (or the fraction of the prey available to predation) by some mechanism (possibly random search). If the prey bursts are sufficiently poor or infrequent for the available prey to be entirely consumed, each predator obtains a share inversely proportional to the number of predators. The resulting response, when calculated on the slow scale, is therefore linear for low values of N/P . On the contrary, if the prey bursts are very rich, the predators are saturated. This imposes an upper asymptote for high values of N/P . Intermediate responses for intermediate ratios complete the curve. Prey reproduction is assumed to be accomplished by a constant fraction of the prey that are inaccessible to predators. An example of such refuging is given by Hassell (1976, p. 33). Flour moth caterpillars are protected from their parasitoid enemies when they are sufficiently deep in the flour to be out of reach of the ovipositor. In this way, a fixed proportion αN of the hosts will be attacked, and the *per capita* attack rate will be $\alpha N/P$. Other examples could be piscivorous birds that can only prey upon the upper layer of fish schools, plants that have a non-edible fraction, etc.

The feeding method used by Slobodkin in his classical experimental studies of long term dynamics of *Daphnia* (1954) and hydras (1964) follow this kind of pattern. The populations were fed daily, what can be considered as continuous feeding with respect to these animals' life cycle, but the food supply was exhausted within a short time (3–4 hr with *Daphnia* and 30 min with hydras). This forces a sharing

mechanism, and therefore a trophic function of the form $g = g(N/P)$. The necessary refugia are simply provided by a separate container for raising the prey.

These simple examples are certainly not the only possible causes of ratio-dependence. This should also be favored by factors like mutual interference, simple refugia, proportional refugia, temporal refugia, non-random search, and other aspects of spatial and temporal heterogeneity. As diverse as these behavioral processes can be on the microscopic scale, and although they may occur as discrete events on this

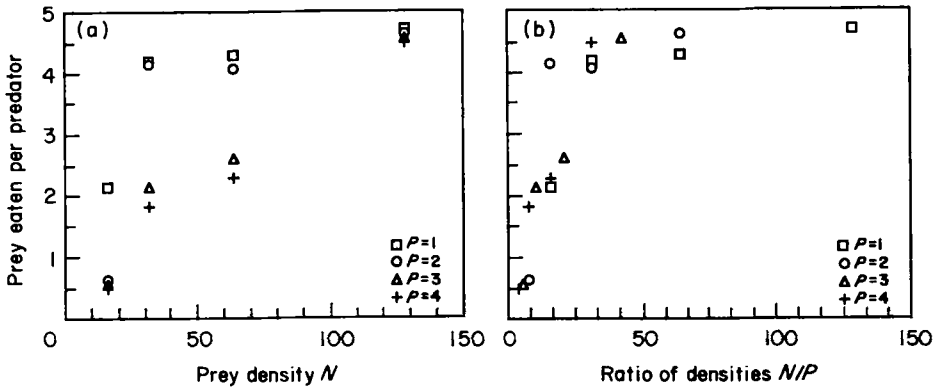


FIG. 2. A marine system studied in the field. Number of prey (barnacles *Balanus balanoides*) eaten per predator (snails *Urosalpinx cinerea*) in 24·7 hr, at different prey densities N and predator densities P . The data points align on a single curve much better when plotted against the ratio N/P (b) than when plotted against N (a) (data from Katz, 1985).

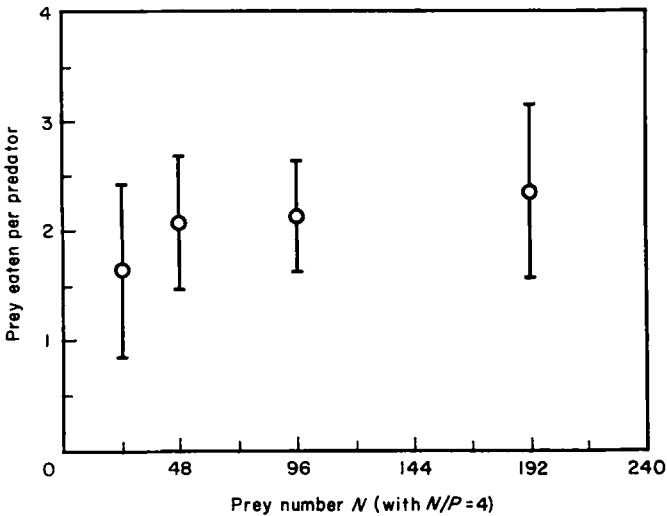


FIG. 3. A mite system in a heterogeneous experimental environment. Number of prey (*Tetranychus urticae*) eaten per predator (*Phytoseiulus persimilis*) in 24 hr, when prey and predator densities are varied in a constant ratio of 4:1. There is no significant difference (after Bernstein, 1981).

scale, we hold that they have a cumulative effect that can be rendered, in the continuous setting of the macroscopic scale, by the single function $g(N/P)$.

Apart from these theoretical considerations, a number of empirical data strongly support the ratio-dependent form. R. Arditi & H. R. Akçakaya (unpublished results) have analyzed several predation experiments where the consumption rate was observed for various numbers of predators and prey. They found that previously published values of mutual interference suffered an underestimation bias and that, after correction, the ratio-dependent form could be used for the trophic function. As an example, Fig. 2 presents the observations of Katz (1985). It is clear that the form $g(N/P)$ represents the data far better than the form $g(N)$. Another evidence is provided by A. A. Berryman (personal communication) who reports two cases of field observations where the growth rate of herbivores and parasitoids can be plotted as a linear function of the consumer/resource ratio. Finally, Fig. 3 presents the results of an experiment using an acarine predator-prey system in a complex environment (Bernstein, 1981). When the numbers of prey and predators were varied with a constant ratio of 4:1, the number of prey eaten per predator did not vary significantly.

The Models

The general model for predator-prey dynamics, in its classical form of first order differential equations, can be written as

$$\frac{dN}{dt} = f(N)N - g(N, P)P \quad (3)$$

$$\frac{dP}{dt} = h(N, P)P - \mu P \quad (4)$$

where $f(N)$ is the *per capita* rate of increase of the prey in the absence of predation and μ is the food-independent predator mortality, assumed to be constant. The function g describes the amount of prey consumed per predator per unit time, while h describes predator production *per capita*. There is ample evidence that predator production can be modeled, to a very good approximation, as simply proportional to food intake

$$h(N, P) = eg(N, P) \quad (5)$$

where e is the conversion efficiency. Specific examples are given by Slobodkin (1986) for hydras, by Beddington *et al.* (1976) for numerous arthropods, and by Coe *et al.* (1976) for large African herbivores. Normally, a minimum threshold reflecting maintenance needs should be subtracted from g in eqn (5), but this can be ignored since its effect can be incorporated into the predator death rate μ in eqn (4). Equation (5) makes the trophic function $g(N, P)$ the sole link between prey and predator dynamics.

For the eqns (3-5) to be internally consistent, $g(N, P)$ must be interpreted as an average rate of consumption over an interval of time on the order of a generation: in an ecological context where continuity is certainly an approximation, the subtraction in eqn (3) can only make sense if both terms describe rates on the same time

scale; the same is true for the two sides of eqn (5). As explained in the Introduction, we propose to examine the hypothesis that the rate of consumption may be modeled as $g = g(N/P)$ when it is averaged on a slow time scale, comparable to that of reproduction.

The following analysis applies to concave increasing functions $g(N/P)$ (Fig. 1). Convex functions (e.g. sigmoid or with a threshold) require a specific analysis but do not lead to any important property qualitatively different from those that will be examined in the rest of the paper. Particular models with ratio-dependent trophic functions have been studied by Ginzburg *et al.* (1971, 1974), Arditi (1975, 1979), Arditi *et al.* (1977, 1978), Getz (1984), Ginzburg (1986), Akçakaya *et al.* (1988). An early use of ratio-dependence was done by Leslie (1948) who built such a model for the predator equation, while keeping the Lotka-Volterra equation for the prey—strangely ignoring any relationship between the rate at which prey are killed and the rate at which predators reproduce (Maynard Smith, 1974, p. 24).

We next compare the static and dynamic properties of the general prey-dependent model

$$\frac{dN}{dt} = f(N)N - g(N)P \quad (6)$$

$$\frac{dP}{dt} = eg(N)P - \mu P \quad (7)$$

vs. the general ratio-dependent model

$$\frac{dN}{dt} = f(N)N - g\left(\frac{N}{P}\right)P \quad (8)$$

$$\frac{dP}{dt} = e g\left(\frac{N}{P}\right)P - \mu P. \quad (9)$$

Comparative Analysis of the Two Types of Systems

The analysis can be performed graphically by the isocline method. Prey-dependent models were analyzed by Rosenzweig (1969, 1971). The predator isocline, obtained by setting eqn (7) equal to zero, is always vertical and its position is

$$A = g^{-1}\left(\frac{\mu}{e}\right) \quad (10)$$

where g^{-1} is the inverse function of g . Because g^{-1} is monotonic, A decreases with increasing predator efficiency e . The prey isocline, obtained by setting eqn (6) to zero, can be “humped” or not. The hump cannot appear if the slope of $g(N)$ at the origin, a , is relatively low. The equilibrium is unstable and gives rise to limit cycles if the isoclines intersect on the ascending part of the prey isocline. If μ/e is greater than the upper asymptote of g , A does not exist and predators can never grow. The humped case is usually considered as generic since it includes all dynamical behaviors of the non-humped case.

In the ratio-dependent model, the total predator consumption satisfies the inequality

$$g\left(\frac{N}{P}\right)P \leq \alpha N \quad (11)$$

because of the concavity of g , and irrespective of the predator abundance; α is the slope of $g(N/P)$ at the origin. Figure 4 shows the construction of the prey isocline. It is given by the intersections of the prey production curve $f(N)N$ and the family of consumption curves $g(N/P)P$, plotted against N . The inequality (11) means that the consumption curves are limited by the line αN . As in the prey-dependent model, two cases must be considered according to α . If the limiting consumption line crosses the production curve, the prey equilibria are limited by a lower value N_L [Fig. 4(a)]. For prey densities under this value, prey production is always greater than the maximum amount that may be consumed. For this reason, we call this case "limited predation". In the case of high α [Fig. 4(b)], the limitation on the consumption rate has practically no effect: at any prey density, more prey may be consumed than can be produced, if there are enough predators.

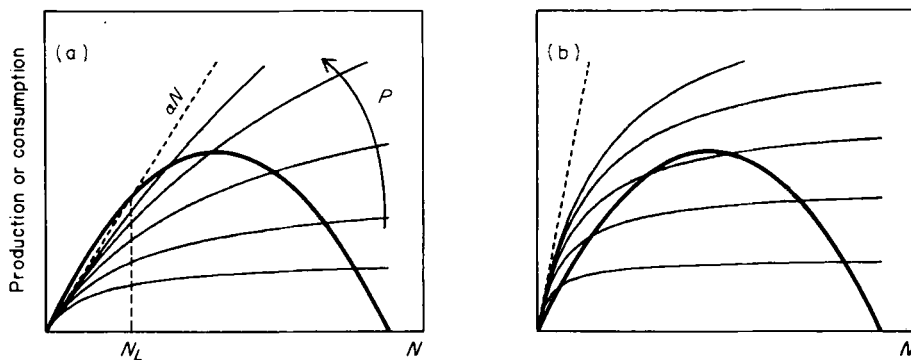


FIG. 4. Possible values of prey equilibria in ratio-dependent models. The thick curve is prey production. The family of light curves are consumptions by increasing numbers of predators. For a fixed value of P , the prey equilibrates where consumption equals production. The consumption curves all start with the same slope α . (a) If α is small, the prey equilibria cannot be lower than N_L ; this is the "limited predation" case. (b) If α is large enough, all prey values are possible equilibria.

The isoclines of ratio-dependent models are presented on Fig. 5. The prey isocline is very different depending on α . If α is small, the prey equilibrium cannot drop lower than the value N_L , as was seen on Fig. 4(a). As a result, the prey isocline has a vertical asymptote [Fig. 5(a)]. If α is large, the consumption curves cross the prey production curve twice, as was shown on Fig. 4(b), and the prey isocline is always humped and passes through the origin [Fig. 5(b)]. The predator isocline is a straight line passing through the origin, with a slope equal to $1/A$, where A is defined as above. This slope increases with increasing predator efficiency. In the case of limited predation, the equilibrium always exists and is always stable. In the other case, the equilibrium is unstable and gives rise to limit cycles if the isocline intersection lies on the ascending part of the prey isocline. If the predator isocline is very steep, the

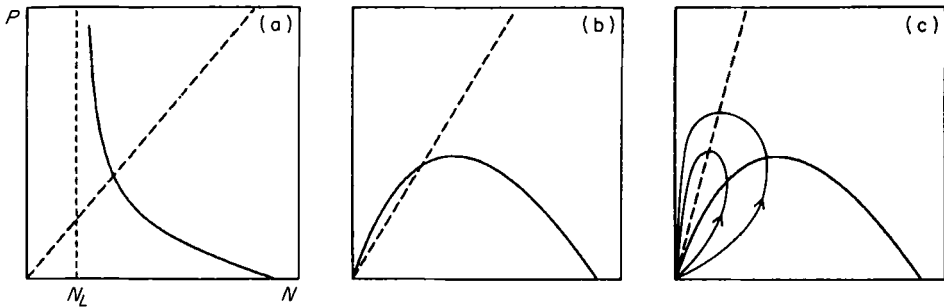


FIG. 5. Isocline analysis of ratio-dependent models. The predator isocline is always a slanted line. (a) In the "limited predation" case, the prey isocline has a vertical asymptote at N_L ; the equilibrium point is always stable. (b) If predation is not limited, the prey isocline is always humped; the equilibrium point is unstable if it lies on the ascending part of the hump. (c) For very efficient predators, the only equilibrium point is the origin which is a global attractor; typical trajectories are presented.

isoclines intersect only at the origin, which is a higher order global attractor [Fig. 5(c)]. As in the prey-dependent model, the case of high α must be considered as generic.

In summary, increasing the conversion efficiency e moves to the left the vertical predator isocline of the prey-dependent model, and makes steeper the slanted predator isocline of the ratio-dependent model. For low efficiencies, the outcomes of the models do not differ very much. In both models, there is a minimal efficiency under which A does not exist: predators become extinct and the prey stabilize at the carrying capacity. Above this minimal value, the equilibrium point first lies on the rightmost part of the prey isocline. In both models, the predator equilibrium increases while the prey equilibrium decreases. The models differ for higher efficiencies. In the prey-dependent model, the prey equilibrium can tend to zero while the predator equilibrium tends to a positive constant. In the ratio-dependent model, a parallel effect of the predator-prey ratio tending to infinity exists only in the limited predation case (low α): Fig. 5(a) shows that when the predator isocline becomes steeper, the prey equilibrium tends to the constant N_L , and the predator tends to infinity. In the generic case of large α , both equilibria decrease as the slope increases [Fig. 5(b)], and both populations become extinct above a maximal conversion efficiency [Fig. 5(c)]. Thus, the ratio-dependent model can describe the extinction of the system by complete prey exhaustion; the prey-dependent model is unable to generate this outcome. In both models, limit cycles can arise when the conversion efficiency exceeds a certain critical value.

The preceding graphical description can be confirmed by an analytical study of the specific systems obtained from eqns (6)-(7) and eqns (8)-(9) by choosing for instance the "disc" model (Holling, 1959b) for g (Arditi, 1979; Getz, 1984).

Response to Primary Production

Further contrasts between the two models are revealed by the response of population equilibria to variations in prey production. In prey-dependent models, the prey

equilibrium is entirely determined by the predator equation. It does not depend in any way on the rate of prey production. In ratio-dependent models, on the contrary, the predator equation determines the equilibrium *ratio*; the equilibrium values of both populations depend on prey production. More precise statements can be made by considering different types of prey production.

EXTERNAL PREY INPUT

If the prey production term $f(N)N$ is replaced by an exogeneous input flux F , the equilibrium values become the following for the prey-dependent case:

$$N^* = A$$

$$P^* = \frac{e}{\mu} F$$

and for the ratio-dependent case:

$$N^* = \frac{Ae}{\mu} F$$

$$P^* = \frac{e}{\mu} F$$

where the parameter A given by eqn (10) is independent of the input flux.

Increasing the external input does *not* increase the prey equilibrium in the prey-dependent model, while the ratio-dependent model shows a proportionate response of both populations. The response of the predator equilibrium is identical in both models.

LOGISTIC GROWTH

If the prey production follows the logistic growth $f(N) = r(1 - N/K)$, the population equilibria are in the case of prey-dependence

$$N^* = A$$

$$P^* = \frac{Aer}{\mu} \left(1 - \frac{A}{K}\right)$$

and in the case of ratio-dependence

$$N^* = K \left(1 - \frac{\mu}{erA}\right)$$

$$P^* = \frac{K}{A} \left(1 - \frac{\mu}{erA}\right).$$

The responses are similar to the case of an external input; if, for whatever reason, prey production is improved by increasing r or K , it will benefit the predator alone in prey-dependent models, while both equilibria will increase in ratio-dependent models.

CONTROLLED PREY ABUNDANCE

If the prey abundance is artificially maintained at a constant level \bar{N} different from the equilibrium N^* , the prey-dependent model has no predator equilibrium: the predators will either grow (if $\bar{N} > N^*$) or decline (if $\bar{N} < N^*$) exponentially. In the ratio-dependent model, however, they equilibrate at a level proportional to \bar{N} :

$$P^* = \frac{\bar{N}}{A}$$

Table 1 summarizes the responses in these different conditions. In every case the predictions of the prey-dependent model seem to apply to homogeneous systems with fast dynamics while the ratio-dependent model seems to give more reasonable predictions for heterogeneous systems with slow dynamics, like large terrestrial carnivores and their prey.

TABLE 1

Responses to changes in prey production. Arrows show the variation of prey and predator equilibria, in the two types of models. Symbols: → no response; ↗ proportionate response; ↑ weakly increasing response

Cause	Prey-dependence		Ratio-dependence	
	N^*	P^*	N^*	P^*
Increase of F	→	↗	↗	↗
Increase of K	→	↗	↑	↑
Increase of r	→	↑	↗	↗
Maintained $\bar{N} < N^*$		to 0		to \bar{N}/A
Maintained $\bar{N} > N^*$		to ∞		to \bar{N}/A

Food Chains

The two types of models also show striking differences in the properties of population equilibria in food chains of increasing length. For simplicity, let us assume that the production of the first level is controlled by an exogeneous input flux F , and that only the last level suffers the non-predatory mortality μ . Alternately, the first-level production could be assumed to follow the logistic law, but this complicates the calculations without bringing any new qualitative feature, as we have already shown for the two-level system.

Table 2 shows the responses of the different trophic levels to variations of the input flux F in the two types of models. In the ratio-dependent model, all levels respond proportionately to F . In the traditional prey-dependent model, the responses are extremely different depending on the level and on the number of levels. The only level that responds proportionately to F is the last, top predator, level. The next to the last always remains *constant*. The lower levels can even *decrease* with

TABLE 2

Responses of food chains to primary input F . Arrows show the variation of population equilibria to an increase of F , in food chains of length 2 to 5, in the two types of models. Symbols: \rightarrow no response; \nearrow proportionate response; \uparrow non-linear increasing response; \downarrow non-linear decreasing response

Level	Prey-dependence				Ratio-dependence			
	2	3	4	5	2	3	4	5
N^*	\rightarrow	\uparrow	\downarrow	\uparrow	\nearrow	\nearrow	\nearrow	\nearrow
P_1^*	\nearrow	\rightarrow	\uparrow	\downarrow	\nearrow	\nearrow	\nearrow	\nearrow
P_2^*		\nearrow	\rightarrow	\uparrow		\nearrow	\nearrow	\nearrow
P_3^*			\nearrow	\rightarrow			\nearrow	\nearrow
P_4^*				\nearrow				\nearrow

increasing primary production. Additionally, chains longer than two levels cannot reach an equilibrium when F exceeds a certain critical value.

Discussion

DYNAMICAL PROPERTIES

The graphic expression of ratio-dependence is the slanted predator isocline and possibly the vertical asymptote of the prey isocline (e.g. Emlen, 1984, pp. 110–118; Taylor, 1984, pp. 70–81; Begon *et al.*, 1986, pp. 361–366). We have seen that these systems can have different dynamical patterns according to whether they have “limited predation” or not, i.e. whether α is small or large.

In limited predation systems, the total amount of prey killed by all predators $g(N/P)P$ cannot exceed αN and it tends to this value for small N and large P . In other words, the amount of prey made available to predators is only determined by prey density. This has a similarity to the “donor control” mechanism described and modeled by Pimm (1982, p. 16). In this model, the predators only consume dying prey. They do not affect the prey equilibrium, which would remain unchanged were the predators removed. As far as the prey equation is concerned, this is, in fact, a very special case of limited predation in which the value of α is equal to zero, making N_L equal to the carrying capacity K [see Fig. 4(a)]. Donor control is therefore a case of ratio-dependence but not a necessary consequence of it, and it is probably rare, as discussed by Pimm (1982, p. 96). In the general situation where $N_L < K$, predator removal leads to an increase in prey equilibrium. In summary, in ratio-dependent models, the number of prey “offered” to predators is “controlled” by the prey, but the level of prey equilibrium does react to predator removal.

When the limited predation condition does not hold (large α), the stability pattern of the system becomes closer to that of a prey-dependent system, although by no means identical. Stability depends above all on the conversion efficiency e , and limit

cycles can arise for efficient predators. Thus, both conversion efficiency e and capturing efficiency α have a destabilizing effect, as in prey-dependent models.

Population equilibria of both prey and predators decrease with increasing conversion efficiency, and with very efficient predators the only possible outcome is complete extinction of the system: the predators die out after exhausting the prey. This very reasonable outcome of predation, routinely observed in the laboratory (e.g. Gause, 1934), cannot be described by traditional prey-dependent models.

RESPONSES TO PRIMARY INPUT

The responses of the two types of systems to variations in prey production differ sharply. Ratio-dependent models predict proportional increases of both populations, while prey-dependent models predict that only predators benefit from increased prey production. This contrast is due to the shape of the predator isocline which is a vertical line in the case of prey-dependence. Natural cases that seem to present this feature are plankton communities where it has been reported that an increase of primary production can lead to a sharp increase of the zooplankton but not of the phytoplankton, which may even decrease. Other examples are Gause's classical experiments on microbial systems (see Rosenzweig, 1977).

Prey-dependent models with humped prey isoclines present the "paradox of enrichment" (Rosenzweig, 1971) by which an increase in the prey carrying capacity destabilizes the system. Ratio-dependent models do not present this effect if the prey production follows the logistic law, but it can be obtained, very weakly, with other production curves. Again, clear evidence for this effect only comes from chemostat-like microbial systems (Luckinbill, 1973, 1974).

When considering the response of food chains, ratio-dependence predicts that all levels would benefit from increased primary production. On the contrary, prey-dependent models predict that in similar environments differing in the primary production, the top carnivores would be more numerous in the richer places, while the standing biomass of their prey would not differ. Very clear evidence supporting the ratio-dependent hypothesis is given by Ricklefs (1979, p. 623) who shows that wolf populations and their prey vary among localities in the same biomass ratio.

The concepts of population regulation "from above" and "from below" are associated to prey-dependence. Because of the vertical predator isocline, the prey equilibrium is necessarily determined by the predators (i.e. from above), while the predator equilibrium is determined by the height of the prey isocline (i.e. from below). In the ratio-dependent model, on the other hand, the characteristics of both populations jointly determine both population equilibria because of the slanted predator isocline. If the slope of this isocline is low, the system can be viewed as being essentially "bottom-up controlled" because it will be very sensitive to the prey carrying capacity. For steeper slopes, predator characteristics play an increasing part and the system becomes more "top-down controlled". However, all intermediate situations exist, making these concepts rather inadequate.

The prey-dependent model underlies the famous HSS theory to explain why the world is "green" (Hairston *et al.*, 1960): being regulated by the carnivores, the

herbivores are unable to devastate the vegetation. The same hypothesis was later generalized by Fretwell (1977): trophic chains with an odd number of levels would produce "green" ecosystems (top-down controlled), while even numbers would produce "brown" ecosystems (bottom-up controlled). This property is akin to the alternating pattern shown by Table 2. The crucial importance attached to the parity of the chain length is disturbing. In ratio-dependent models, on the contrary, the abundance of any level can be high or low for any chain length. "Green" or "brown" systems can exist for any length, the "color" being determined by the full set of parameters and, in particular, by factors related to primary productivity.

In principle, a simple qualitative observation could be made that would help assess the proposed ratio-dependent form: resource richer but otherwise similar ecosystems should exhibit higher equilibrium abundances on all trophic levels, including the amount of unused primary resource. This seemingly reasonable expectation is in complete contradiction with the prey-dependent model. On one hand, a possible illustration is given by the worldwide comparison of forest ecosystems done by Whittaker (1975, pp. 224-226). Forests of increasing productivity show a responding pattern both in plant and animal biomasses (Fig. 6). On the other hand, Oksanen *et al.* (1981) and Oksanen (1983) claimed corroboration of Fretwell's hypothesis in aquatic ecosystems and in tundras. One may consider that these systems are much more homogeneous and uniform than forests. Of course, these gross comparisons are fraught with disputable interpretations because of the difficulties of counting the trophic levels, of evaluating the similarity of different ecosystems, and of ascertaining their state of equilibrium. We trust that much more convincing evidence will be drawn from experiments undertaken in the field as well as in the laboratory.

In conclusion, a number of comparisons between the two types of models indicate that many aspects of ecological theory rely on the particular assumption of prey-dependence. The alternative ratio-dependent form gives in many instances predictions that seem more reasonable. This form is also directly supported by many empirical observations, some of which were presented in the Introduction. We suggest that the traditional prey-dependent form may apply to simple, homogeneous systems with rapid turnovers, comparable to chemostats where predation is essentially a continuous and local process. The ratio-dependent form seems more appropriate in complex, heterogeneous systems where the final, large scale, outcome of predation is a sharing process. We expect that future work will investigate more closely how behavioral and physiological mechanisms must be translated on the large scale of population dynamics, and we hope that accumulation of evidence will allow clear delineation of the areas of applicability of the two opposite idealizations.

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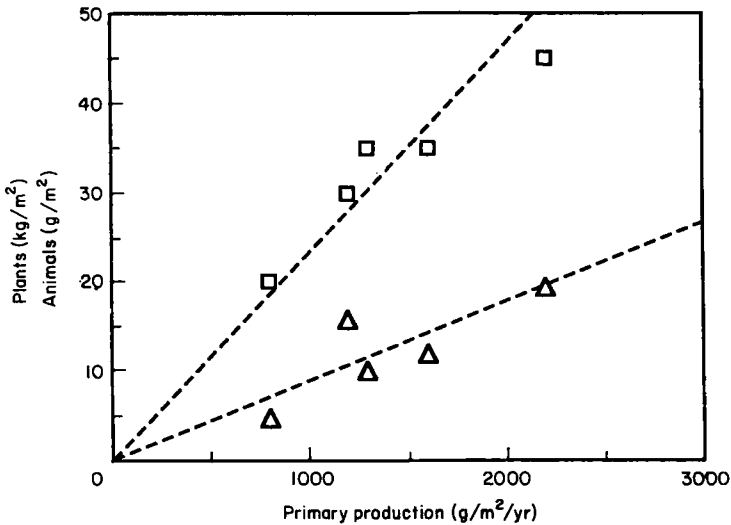


FIG. 6. Standing plant (\square) and animal (Δ) biomasses vs. net annual primary productivity in forest ecosystems (data from Whittaker, 1975). From left to right: boreal forest, temperate deciduous forest, temperate evergreen forest, tropical seasonal forest, tropical rainforest.

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REFERENCES

- AKÇAKAYA, H. R., GINZBURG, L. R., SLICE, D. & SLOBODKIN, L. B. (1988). The theory of population dynamics: II. Physiological delays. *Bull. Math. Biol.* **50**, 503–515.
- ARDITI, R. (1975). *Etude de modèles théoriques de l'écosystème à deux espèces proie-prédateur*. Specialty Doctorate Thesis, University of Paris 7.
- ARDITI, R. (1979). *Les composants de la prédation, les modèles proie-prédateur et les cycles de populations naturelles*. State Doctorate Thesis, University of Paris 7.
- ARDITI, R. (1983). A unified model of the functional response of predators and parasitoids. *J. anim. Ecol.* **52**, 293–303.
- ARDITI, R., ABILLON, J.-M. & VIEIRA DA SILVA, J. (1977). The effect of a time-delay in a predator-prey model. *Math. Biosci.* **33**, 107–120.
- ARDITI, R., ABILLON, J.-M. & VIEIRA DA SILVA, J. (1978). A predator-prey model with satiation and intraspecific competition. *Ecol. Modelling* **5**, 173–191.
- BEDDINGTON, J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *J. anim. Ecol.* **44**, 331–340.
- BEDDINGTON, J. R., HASSELL, M. P. & LAWTON, J. H. (1976). The components of arthropod predation. II. The predator rate of increase. *J. anim. Ecol.* **45**, 165–186.
- BEGON, M., HARPER, J. L. & TOWNSEND, C. R. (1986). *Ecology: Individuals, Populations and Communities*. Oxford: Blackwell.
- BERNSTEIN, C. (1981). *Dispersal of Phytoseiulus persimilis [Acarina: Phytoseiidae] in Response to Prey Density and Distribution*. D. Phil. Thesis, Oxford University.
- COE, M. J., CUMMING, D. H. & PHILLIPSON, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* **22**, 341–354.
- CURRY, G. L. & FELDMAN, R. M. (1987). *Mathematical Foundations of Population Dynamics*. College Station: Texas A & M University Press.
- DEANGELIS, D. L., GOLDSTEIN, R. A. & O'NEILL, R. V. (1975). A model for trophic interaction. *Ecology* **56**, 881–892.
- EMLEN, J. M. (1984). *Population Biology*. New York: Macmillan.

- FREE, C. A., BEDDINGTON, J. R. & LAWTON, J. H. (1977). On the inadequacy of simple models of mutual interference for parasitism and predation. *J. anim. Ecol.* **46**, 543-554.
- FRETWELL, S. D. (1977). The regulation of plant communities by the food chains exploiting them. *Perspect. Biol. Med.* **20**, 169-185.
- GAUSE, G. F. (1934). *The Struggle for Existence*. Baltimore: Williams and Wilkins. (Reprint, 1971, New York: Dover.)
- GETZ, W. M. (1984). Population dynamics: a *per capita* resource approach. *J. theor. Biol.* **108**, 623-643.
- GINZBURG, L. R. (1986). The theory of population dynamics: I. Back to first principles. *J. theor. Biol.* **122**, 385-399.
- GINZBURG, L. R., GOLDMAN, YU. I. & RAILKIN, A. I. (1971). A mathematical model of interaction between two populations. I. Predator-prey. *Zh. Obshch. Biol.* **32**, 724-730 (in Russian).
- GINZBURG, L. R., KONOVALOV, N. YU. & EPELMAN, G. S. (1974). A mathematical model of interaction between two populations. IV. Comparison of theory and experimental data. *Zh. Obshch. Biol.* **35**, 613-619 (in Russian).
- HAIRSTON, N. G., SMITH, F. E. & SLOBODKIN, L. B. (1960). Community structure, population control, and competition. *Am. Nat.* **94**, 421-425.
- HASSELL, M. P. (1976). *The Dynamics of Competition and Predation*. London: Edward Arnold.
- HASSELL, M. P. (1978). *The Dynamics of Arthropod Predator-Prey Systems*. Princeton: Princeton University Press.
- HASSELL, M. P., LAWTON, J. H. & BEDDINGTON, J. R. (1977). Sigmoid functional responses by invertebrate predators and parasitoids. *J. Anim. Ecol.* **46**, 249-262.
- HOLLING, C. S. (1959a). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Ent.* **91**, 293-320.
- HOLLING, C. S. (1959b). Some characteristics of simple types of predation and parasitism. *Can. Ent.* **91**, 385-398.
- KATZ, C. H. (1985). A nonequilibrium marine predator-prey interaction. *Ecology* **66**, 1426-1438.
- KUNO, E. (1987). Principles of predator-prey interaction in theoretical, experimental, and natural population systems. *Adv. Ecol. Res.* **16**, 250-337.
- LESLIE, P. H. (1948). Some further notes on the use of matrices in population mathematics. *Biometrika* **35**, 213-245.
- LUCKINBILL, L. S. (1973). Coexistence in laboratory populations of *Paramecium aurelia* and its predator *Didinium nasutum*. *Ecol.* **54**, 1320-1327.
- LUCKINBILL, L. S. (1974). The effects of space and enrichment on a predator-prey system. *Ecology* **55**, 1142-1147.
- MAY, R. M. (1973). *Stability and Complexity in Model Ecosystems*. Princeton: Princeton University Press.
- MAYNARD SMITH, J. (1974). *Models in Ecology*. Cambridge: Cambridge University Press.
- MURDOCH, W. W. & OATEN, A. (1975). Predation and population stability. *Adv. Ecol. Res.* **9**, 1-131.
- OKSANEN, L. (1983). Trophic exploitation and arctic phytomass patterns. *Am. Nat.* **122**, 45-52.
- OKSANEN, L., FRETWELL, S. D., ARRUDA, J. & NIEMELÄ, P. (1981). Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* **118**, 240-261.
- PIMM, S. L. (1982). *Food Webs*. London: Chapman and Hall.
- RICKLEFS, R. E. (1979). *Ecology*. (2nd ed.) New York: Chiron Press.
- ROSENZWEIG, M. L. (1969). Why the prey curve has a hump. *Am. Nat.* **103**, 81-87.
- ROSENZWEIG, M. L. (1971). Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science, N. Y.* **171**, 385-387.
- ROSENZWEIG, M. L. (1977). Aspects of biological exploitation. *Q. Rev. Biol.* **52**, 371-380.
- ROSENZWEIG, M. L. & MACARTHUR, R. H. (1963). Graphical representation and stability conditions of predator-prey interactions. *Am. Nat.* **97**, 217-223.
- ROYAMA, T. (1971). A comparative study of models for predation and parasitism. *Res. Pop. Ecol.* (Suppl. 1.)
- SLOBODKIN, L. B. (1954). Population dynamics in *Daphnia obtusa* Kurz. *Ecol. Monogr.* **24**, 69-87.
- SLOBODKIN, L. B. (1964). Experimental populations of Hydrida. *J. anim. Ecol.* **33**(Suppl.), 131-148.
- SLOBODKIN, L. B. (1986). The role of minimalism in art and science. *Am. Nat.* **127**, 257-265.
- SVIREZHEV, YU. M. & LOGOFET, D. O. (1983). *Stability of Biological Communities*. (English ed.) Moscow: Mir Publishers.
- TAYLOR, R. J. (1984). *Predation*. London: Chapman and Hall.
- WHITTAKER, R. H. (1975). *Communities and Ecosystems*. (2nd ed.) New York: Macmillan.
- WIENS, J. A., ADDICOTT, J. F., CASE, T. J. & DIAMOND, J. (1986). Overview: the importance of spatial and temporal scale in ecological investigations. In: *Community Ecology*. (Diamond, J. & Case, T. J., eds) pp. 145-153. New York: Harper and Row.