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Interference and Generation Cycles

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In this paper we re-examine the derivation of an interference limited functional response due to Beddington (1975 *J. Anim. Ecol.* **44**, 331–340) and extend his treatment to more realistic models of the interference process. We study the dynamic effects of interference in the context of a structured population model and show that the stabilising effect of interference against paradox of enrichment cycles is unaffected by age-structure. We also demonstrate that single generation cycles are much more weakly affected by interference than prey-escape cycles. Thus the net effect of weak interference is to prevent single generation cycles from being masked by the prey-escape cycles which would otherwise dominate the population dynamics. © 1992 Academic Press, Inc.

INTRODUCTION

Simple predator-prey models with self-limiting prey and a non-linear predator functional response very commonly become destabilised as the prey carrying capacity is increased. They then exhibit large amplitude limit cycles in which the prey numbers increase out of control until limited by their own carrying capacity, subsequently the more slowly increasing predator numbers reach a level where predation wipes out the majority of the prey population and the process begins again. Cycles generated by this mechanism, which De Roos *et al.* (1990) have called “prey-escape”, typically have very large amplitudes, with prey numbers being driven to many orders of magnitude below their average abundance in the trough of the cycle. The occurrence of “prey-escape” cycles under conditions of high prey carrying capacity has been termed the “paradox of enrichment” (Rosenzweig, 1971).

Many mechanisms have been proposed to explain the relative scarcity of large amplitude predator-prey cycles in natural systems, one of the earliest being direct dependence of the predator functional response on predator density (Hassell and Varley, 1969). Such direct density dependence could arise in many different ways, ranging from aggressive predator-predator interactions of the kind discussed by Beddington (1975) to pseudo-interference (Free *et al.*, 1977) resulting from aggregative behaviour in a spatially inhomogeneous environment. Recently, in a series of papers, Arditi and co-workers Arditi and Ginsburg, 1989; Arditi and Akcakaya, 1990; Arditi *et al.*, 1991 have argued for ratio-dependent predation as a resolution of the paradox of enrichment.

Beddington's (1975) treatment of the process of interference limited predation in a homogeneous environment is flawed in several important regards. First, he assumes that predators interfere with each other in an identical way at all times (even when already engaged in another interaction). Second, his treatment of the statistics of the predator-predator interaction neglects the fact that each predator-predator encounter removes not one but two predators from the sub-population engaged in searching for food. We begin this paper by examining a series of detailed behavioural models of the predation process in a homogeneous environment. We develop a novel form of uptake function appropriate to the case where only searching individuals can interact, and show that the Beddington form of functional response is obtainable as an approximation in the cases where individuals can interact with feeding or interacting individuals.

We then examine the dynamic effects of our candidate uptake functions in both a structured and an unstructured population model. Our primary aim in this part of the work is to compare the stabilising effects of interference in the context of single-generation cycles with that seen in the context of prey-escape cycles. The population model we use is derived from that used by Gurney and Nisbet (1985) in their study of the relationship between the expression of juvenile competition and the period of population cycles. In this case the predator population is controlled by food dependent juvenile mortality, and when adult lifetime is short the model exhibits large amplitude cycles with a period of a little over one developmental delay.

These "single-generation cycles" are differentiated from prey-escape cycles by their dependence on model parameters. The frequency of prey-escape cycles depends on the characteristics of both predator and prey. The frequency of a cycle of single generation type depends almost exclusively on predator characteristics (developmental delay and to a lesser extent death rate) and is very insensitive to changes in prey parameters.

We find that the stabilising action of interference against prey-escape cycles in the age-structured models is essentially similar to (albeit a little

stronger) than that seen in the equivalent unstructured model. If the interference is stronger than a (low) threshold level no degree of enrichment (increase in carrying capacity) can result in predator-prey cycles. However, single-generation cycles are very much less sensitive to the effects of direct density dependence than prey-escape cycles. For many parameter sets mild enrichment will send the structured models into single-generation cycles irrespective of the strength of interference. Even where interference can stabilise single-generation cycles, much higher levels are required than are needed to remove the prey escape cycles.

We conclude that in our model the presence of age-structure effects does not alter the perception that small amounts of direct density dependence can eliminate the paradox of enrichment. However, populations with the characteristics required for the production of single-generation cycles (immediate expression of competition, short reproductive lifetime) will exhibit such cycles irrespective of the presence of considerable direct density dependence in the functional response.

THE FUNCTIONAL RESPONSE

In the elementary theoretical treatment of functional response it is assumed that the prey population is distributed uniformly, at density F , within an arena of fixed volume. The prey are attacked by randomly searching predators whose population density is P . Each predator is assumed to explore a (fixed) volume V_s per unit time, and when a predator attacks a prey individual it is assumed to refrain from further searching for a "handling time" t_h . The treatment of interference originally due to Beddington (1975) further assumes that if two predators meet, the ensuing interaction prevents *both* from engaging in other activities for a fixed "face-off time" t_w . The rate at which such predator-predator encounters occur is assumed to be proportional to the predator density—an approximation which not only rests on the view that a given predator interacts equally with all others, but also carries the hidden assumption that only one predator is mobile at any given instant.

To avoid these difficulties we adopt an approach borrowed from chemical reaction kinetics. We divide the predator population into sub-populations according to their current activity, so that the density of searching individuals is S , that of individuals engaged in handling prey is H , and that of individuals involved in aggressive encounters with other predators is W . We assume that these states are mutually exclusive so that

$$S + H + W = P. \quad (1)$$

We write down a set of transition rules between the states, which enables us to formulate a set of differential equations describing their dynamics. In order to simplify these dynamic equations, we assume that both aggressive interaction and prey capture takes place on a timescale much shorter than predator birth and death processes. Although this implies the restrictive assumption that aggressive interactions do not contribute *directly* to the predator death rate, it brings with it the substantial benefit that, over the timescale of interest, we can take the total population P to be constant. It further implies that we can safely deduce the average proportion of a predator's time spent searching (S^*/P) from the steady state solution of these dynamic equations. We thus calculate the food uptake per unit time per predator (the functional response) from

$$I(F, P) = V_s (S^*/P) F. \quad (2)$$

For the case where only searching individuals can become involved in aggressive interactions the rules and the ensuing differential equations are particularly simple. If we denote an individual in state X by X_i , and an individual food item by F_i , then food uptake is described by the "reaction"

predator-predator encounters by

and the "decay" of handling or interfering individuals back to the searching state by

Equations (3) and (4) represent second-order processes which proceed at a rate proportional to the product of the densities of the two "reactants"—the constant of proportionality being the volume search rate V_s . If we assume that the times spent by an individual on any given visit to the "handling" or "interacting" states are exponentially distributed random variables with mean values t_h and t_w , respectively, then Eqs. (5) and (6) represent first-order processes with time constants t_h and t_w , respectively. With the aid of the conservation condition (Eq. (1)) we can now see that the balance equations for the sub-populations H and S are

$$dH/dt = V_s S F - H/t_h \quad (7)$$

$$dS/dt = -V_s S F - 2V_s S^2 + H/t_h + (P - S - H)/t_w. \quad (8)$$

The assumption of a fast timescale allows us to consider only the steady state arising from these equations. We note that this steady state is unaffected by changing from exponential distributions to constant values for the handling and face-off times, although the differential equations then take a different form.

The positive steady-state solution of these equations is

$$S^*/P = [(C+1)/4D][-1 + \sqrt{(1+8D/(C+1)^2)}], \quad (9)$$

where, for compactness we have defined

$$C = V_s t_h F \quad (10)$$

$$D = V_s t_w P. \quad (11)$$

In the general case, the resulting functional response is messy and uninformative, but if we further assume that interference is sufficiently weak (that is, the proportion of time spent in aggressive interactions is sufficiently small) so that $8D \ll (1+C)^2$, then Eq. (9) simplifies to

$$S^*/P = 1/(1+C) - 2D/(1+C)^3, \quad (12)$$

which can be approximated by

$$S^*/P = 1/(1+C+2D/(1+C)), \quad (13)$$

and the functional response takes the form which we hereafter refer to as the search-interaction-only (SIO) form

$$I = I_{\max} F / (F + F_0 + \phi(F) P). \quad (14)$$

In this expression we have used the conventional definitions for the maximum ingestion rate $I_{\max}$ and the half-saturation food density (now applicable only at very small predator populations)

$$I_{\max} = 1/t_h \quad (15)$$

$$F_0 = (1/V_s t_h) \quad (16)$$

and have defined a food-dependent interference strength (Φ) as

$$\phi(F) = (2t_w/t_h)[F_0/(F+F_0)]. \quad (17)$$

The analysis of the cases where a searching predator is assumed to interact either with all other predators or with both searching and handling predators proceeds along exactly parallel lines, albeit with rather more algebraic labour. We show in the Appendix that in both these cases the

exact stationary solution for the proportion of searching predators is a quadratic expression analogous to Eq. (9). In both cases a weak interference assumption similar to that used above, simplifies the functional response to a form closely resembling that derived by Beddington (1975).

Where a searching predator will not interact with con-specifics already involved in aggressive encounters but can interact both with searching and handling individuals, the result is

$$I = I_{\max} F / (F + F_0 + \sigma P), \quad (18)$$

where the interference strength parameter σ is defined as

$$\sigma = 2t_w/t_h. \quad (19)$$

We refer to this form as the Beddington functional response.

Where a searching predator can interact with all other conspecifics the result differs from Eq. (18) only by a factor of 2 in the interference term

$$I = I_{\max} F / (F + F_0 + \frac{1}{2}\sigma P). \quad (20)$$

For the remainder of this paper we adopt the weak-interference approximation, and explore population dynamic implications of the SIO and Beddington functional response curves (14) and (18). As an aid to our analysis we identify two limits in which these responses simplify yet further. The first of these is the "type II limit" in which $t_w \ll t_h$, and both variants of the functional response reduce to the standard Holling type II form (Holling, 1959).

$$I = I_{\max} F / (F + F_0). \quad (21)$$

We refer to the second limit, in which the search volume V_s becomes very large and hence F_0 becomes very small, as the "rapid-searching limit." In this limit the Beddington functional response (Eq. (18)) reduces to the ratio-dependent form advocated by Arditi and Akçakaya (1990), namely,

$$I = I_{\max} / (1 + \sigma P/F). \quad (22)$$

When F_0 is set to zero in the search-interaction-only response (Eq. (14)) it reduces to a constant uptake rate $I = I_{\max}$. This difference in behaviour in the rapid-searching limit is indicative of an underlying difference in the picture of the interaction process implied by our assumptions. In both derivations leading to the Beddington form, a searching individual is assumed to interact with individuals who are handling food. Thus as the search volume V_s becomes very large and hence F_0 tends towards zero, the crucial indicator of interaction frequency, and hence uptake rate, is the

ratio of the food density to the predator density. However, if interaction is restricted to searching individuals only, the probability of interaction is the product of the (finite) density of available partners with a searching time which goes to zero as V_s becomes very large. Thus in this case the interaction rate goes to zero with F_0 , and in this limit the uptake rate is controlled entirely by the handling time.

POPULATION MODELS

Our primary interest in this paper is the interplay between interference in the functional response and the propensity of the population to exhibit either single-generation cycles or predator-prey cycles. We therefore use as our primary testbed a stage-structured model derived from the LD model of Gurney and Nisbet (1985), with the addition of a dynamically linked food source.

The model represents an insect population comprising larvae ($L(t)$) feeding on a food source ($F(t)$) which grows logistically in the absence of predation. The larvae take a fixed time T to develop into adults, but we postulate that their death rate $d(t)$ is inversely proportional to the excess of uptake, $I(t)$, above their maintenance costs (Y), thus

$$d(t) = X/[I(t) - Y]. \quad (23)$$

The uptake rate $I(t)$ is given by either the Beddington functional response, Eq. (18), or the SIO functional response, Eq. (14). The through-stage survival, $S(t)$, of the larvae maturing to adults at time t is

$$S(t) = \exp \left[- \int_{t-T}^t d(x) dx \right]. \quad (24)$$

The adults, $A(t)$, are assumed either not to feed at all, or to feed on some unlimited resource different from that consumed by the larvae. They thus have a density and time-independent per-capita fecundity q and death rate μ . The balance Equations for the three components of the model (adult insects, larvae and food) are thus

$$dA/dt = qA(t-T)S(t) - \mu A(t), \quad (25)$$

$$dL/dt = qA(t) - qA(t-T)S(t) - d(t)L(t), \quad (26)$$

$$dF/dt = rF(t)[1 - F(t)/K] - I(t)L(t). \quad (27)$$

So that we can distinguish effects which depend on age-structure from those which are dependent only upon predator-prey interaction, we also

examine a model which is similar to the model defined by Eqs. (25)–(27) but which does not involve age-structure. Unfortunately, if we employ the apparently appealing procedure of taking the development delay T to zero while maintaining the product $Td(t)$ finite, we obtain a model which makes sense only as rather bad model of cannibalism. We thus choose as our standard of comparison, an unstructured model with the same key features as our structured model: logistic food, density-independent fecundity (Q), and control through changes in per-capita mortality brought about by variations in food uptake rate. Our model thus contains a predator population, $P(t)$, and a food population, $F(t)$, whose dynamics are given by

$$dP/dt = QP(t) - d(t)P(t), \quad (28)$$

$$dF/dt = rF(t)[1 - F(t)/K] - I(t)P(t). \quad (29)$$

The per-capita mortality $d(t)$ is related to the uptake rate $I(t)$ by Eq. (23), and the uptake rate $I(t)$ is given by either the Beddington or the SIO functional response with L replaced by P .

STATICS

We examine first the stationary states (F^* , P^*) of the unstructured model. Equation (28) implies that at a stationary state, the per-capita uptake rate of the predators must take a value (Φ) determined by the parameters X , Y and Q , thus

$$I(F^*, P^*) = (Y + X/Q) \equiv \Phi. \quad (30)$$

The values of F^* and P^* are now given by the intersection of this relationship with the parabola implied by Eq. (29),

$$\Phi P^* = rF^*[1 - F^*/K]. \quad (31)$$

For the Beddington version of the model, Eq. (18) implies that P^* and F^* are related by

$$\Phi P^* = \sigma^{-1}[(I_{\max} - \Phi)F^* - \Phi F_0], \quad (32)$$

while for the SIO version of the model the equivalent relationship is

$$\Phi P^* = \sigma^{-1}[(F^* + F_0)/F_0][(I_{\max} - \Phi)F^* - \Phi F_0]. \quad (33)$$

Both versions of the unstructured model thus have no biologically meaningful (that is positive) non-trivial steady state unless

$$[(I_{\max}/\Phi) - 1] > F_0/K. \quad (34)$$

If this inequality is satisfied, the system has exactly one stationary state with both F^* and P^* strictly positive.

The analysis of the two structured models follows an exactly parallel path. Equation (25) implies that at a stationary state the through-stage larval survival S^* must be equal to the ratio μ/q . Equation (24), however, tells us that $S^* = \exp(-d^*T)$, where from Eq. 23, $d^* = X/(I(F^*, L^*) - Y)$. Thus we see that at a stationary state the per-capita uptake rate of the larvae must take a value (Ω) fixed by the predator parameters (X, Y, T, q, μ), thus

$$I(L^*, P^*) = (Y + XT/\ln[q/\mu]) \equiv \Omega. \quad (35)$$

The food dynamics of the structured models are exactly the same as those of the unstructured model, so Eq. (35) implies a relationship between L^* and F^* which parallels Eqs. 32 (for the Beddington functional response) or (33) (for the SIO response). Thus we see that both versions of the structured model have a single strictly positive stationary state if and only if

$$[(I_{\max}/\Omega) - 1] > F_0/K. \quad (36)$$

We can now identify the relationship between the parameters of the structured and unstructured models which make their equilibria as similar as possible. If $\Omega = \Phi$, that is,

$$Q = T^{-1} \ln[q/\mu], \quad (37)$$

then the structured model (using a given functional response) has the same steady-state food density as its unstructured cousin, as well as a consumer (larval) density equal to the unstructured predator density.

We have so far shown that all four variants of our population model can have only one biologically interesting stationary state in which food and consumers co-exist. The value of the food population at such a steady state is obtained by solving for the positive root of the quadratic equation obtained (for the unstructured models) by combining Eq. (31) with either Eq. (32) or (33) as appropriate. For the Beddington version of the unstructured model this takes the particularly simple form

$$(\sigma r/K)(F^*)^2 + (I_{\max} - \Phi - \sigma r) F^* - \Phi F_0 = 0, \quad (38)$$

from which we see that the behaviour of the solution at very large values of K will depend critically on the relationship of the potential excess uptake ($I_{\max} - \Phi$) to the product of the interference constant and the prey reproduction rate (σr). If

$$\sigma r < (I_{\max} - \Phi), \quad (39)$$

then as the ratio of the carrying capacity to the half-saturation constant (K/F_0) tends to infinity (or more strictly, becomes large compared to $4\Phi\sigma r/(I_{\max} - \Phi - \sigma r)^2$), F^* becomes independent of K , thus

$$F^* = \Phi F_0 / (I_{\max} - \Phi - \sigma r). \quad (40)$$

However if inequality (39) is reversed, then at high carrying capacity the food steady state is directly proportional to the prey carrying capacity (K), thus

$$F^* = K(1 - (I_{\max} - \Phi)/\sigma r). \quad (41)$$

This behaviour is illustrated for a particular set of parameters by the contour plots shown in Figs. 1a and 1b, from which we also note that when interference is strong ($\sigma r/I_{\max}$ is large) the predator steady state P^* decreases in inverse proportion to the strength of interference.

Because Eqs. (31) and (33) both contain quadratic terms, the analog of Eq. (38) for the SIO uptake function is much less amenable to analysis. It is, however, possible to show that, with this uptake function, the food steady state F^* is unconditionally independent of the carrying capacity (K) at high values of K . This difference, as well as the broad similarity of behaviour of the two model variants at moderate values of interference and carrying capacity, is illustrated by the contour plots shown in Fig. 1c.

FIG. 1. Contours of constant steady state values for both unstructured models. (Parameters: $Q/r = 0.21127$, $X/rI_{\max} = 0.002$, $Y/I_{\max} = 0.1$.)

A second difference in behaviour between the two model variants, this time affecting the consumer steady state, is evident from a comparison of Figs. 1b and 1d. Since the SIO uptake function is derived assuming that interactions cease during feeding, we expect that in this model interference should become insignificant at high food levels. This would imply that when high interference and high carrying capacity combine to produce high steady-state food values, further increases in interference cease to influence the consumer steady state, in marked contrast to the behaviour of the Beddington variant, where increasing already high interference always acts to reduce consumer steady states.

DYNAMICS

We have shown that all models discussed in this paper can have at most one steady state with co-existing food and consumer populations. The fate of small fluctuations from this stationary state can be assessed by a conventional neighbourhood stability analysis (Nisbet and Gurney, 1982). For the structured population models this procedure yields a messy characteristic equation which can only be solved numerically. However, in the case of the unstructured models we can obtain analytic stability conditions using the Routh-Hurwitz criteria (May, 1974).

For the variant of the unstructured model with the Beddington uptake function, we find that the non-trivial steady state is locally stable if and only if

$$(F^*/K) + (1 - F^*/K)(\Phi/I_{\max})(\sigma Q^2/X - 1) > 0. \quad (42)$$

Clearly F^* must lie in the range 0 to K , so if

$$\sigma > X/Q^2, \quad (43)$$

then inequality (42) is always satisfied and the local stability of the system is guaranteed. If inequality (43) is not satisfied then enrichment (increasing the carrying capacity) may ultimately destabilise the system if the ratio F^*/K decreases with rising K . We showed in the previous section that if this model variant has an intrinsic food growth rate (r) low enough to satisfy inequality (39), then F^* becomes constant at high values of K . Thus with such parameters, intense enrichment is guaranteed to destabilise the system. However, with large r values F^*/K goes to a finite asymptotic limit as K becomes very large, so the stability of the system is unaffected by further enrichment.

In Fig. 2a we illustrate behavioural regions defined by inequalities (42) and (34). We see that for small values of the interference parameter

FIG. 2. Maps of the dynamic regions of all four models. (Parameters for the unstructured models are as in Fig. 1. The structured models are similar but replace Q/r with $rT=5$, $q/r=22$, $\mu/r=7.65$.)

increasing K is guaranteed to destabilise the system. Numerical investigations show that the system then exhibits a stable limit cycle whose frequency is not unlike that of the oscillatory divergence. These cycles are the normal type of "prey-escape" cycles whose occurrence at high K values is frequently referred to as the "paradox of enrichment" (Rosenzweig, 1971). However, as we would expect from previous work on unstructured predator-prey models with density dependence (Hassell and Varley, 1969; Hassell and May, 1973; Getz, 1984; Arditi and Ginzburg, 1989), increasing interference rapidly stabilises the paradox of enrichment cycles, and indeed provided the interference parameter is above the threshold given by inequality (43), no amount of enrichment can produce instability.

Although we can use the Routh-Hurwitz criteria for the unstructured model with the SIO uptake function, the results are much less simple to interpret than those we obtained for the Beddington variant. However, as we show in Fig. 2b their import is almost identical. Weak interference implies that enrichment can drive the system into large amplitude prey escape cycles, but interference above a threshold value produces unconditional system stability.

The transcendental nature of the characteristic equations for the two

structured variants of our population model implies that we cannot hope to derive closed form stability criteria for these cases. However, the boundary of stability for any given root of the characteristic equation can easily be found by numerical curve following algorithms. In Figs. 2c and 2d we illustrate typical results obtained for the two structured model variants. The boundary of stability for the root corresponding to prey-escape cycles is found in very much the same place as that for the equivalent unstructured model. However, the stability behaviour of the system over most of

FIG. 3. The dynamic regions of the two structured models for three values of X . (Values of $X/rI_{\max}$ are given in the top right corner of each plot, all other parameters are as in Fig. 2.)

the parameter plane under investigation is dominated by a different root, corresponding to an oscillatory disturbance whose period is very close to the developmental delay. Numerical investigations show that in regions where this root is unstable and the prey-escape-cycle root is stable, the system shows self-sustaining single-generation cycles of the type discussed by Gurney and Nisbet (1985). Where both the prey-escape root and the generation-cycle root are unstable, the stable limit cycle is predominantly of the prey-escape type.

For the parameters chosen for Fig. 2, the generation cycle root is destabilised by quite moderate enrichment, irrespective of the strength of predator interference. In Fig. 3 we show the results of an investigation of the variation of this pattern of behaviour with the larval death-rate parameter ($X/rI_{\max}$). Raising this parameter first causes the small bump in the overall stability boundary to extend a long tongue into the generation-cycle region and then moves the upper lobe of the generation-cycle region to rapidly increasing values of carrying capacity (K), this effect being somewhat more marked for the Beddington functional response. This effect proceeds very rapidly as the death-rate parameter (X) increases and has the effect of changing the shape of the generation-cycle stability boundary to a shape which resembles that of the prey-escape-cycle boundary.

We thus conclude that the result that generation cycles cannot be stabilised by interference is dependent upon the choice of auxiliary parameters. However, closer examination of Fig. 3 shows that the general stabilising effect of increasing X acts even more rapidly on the prey-escape cycles than it does upon the generation cycles. Indeed once the transition in generation-cycle behaviour has taken place the lower lobe, of the stability boundary for this root moves downward very little further, whereas the stability boundary for prey-escape cycles moves rapidly to vanishingly small values of interference. Thus we can safely conclude that while mutual interference between predators is a very powerful stabilising influence against the prey-escape cycles characteristic of the paradox of enrichment, it has a generally much weaker stabilising effect on single-generation cycles.

DISCUSSION

In this paper we have compared the effects of predator interference in structured and unstructured population models using uptake functions rigorously derived from three different behavioural models. Except at very high carrying capacity, the dynamics of both types of model seem to be relatively insensitive to the difference between the Beddington and SIO forms of uptake function. Thus, despite the dubious nature of the assump-

tions required to derive the Beddington form, its greater mathematical convenience seems to be bought at a relatively low cost.

It is well known (Hassell and May, 1973; Freedman and Sree Hari Rao, 1983; Erbe and Freedman, 1985) that direct density dependence in the predator uptake function has a strong stabilising effect in unstructured predator-prey models. The unstructured population model discussed in this paper is designed to be as close as possible to the age structured model used by Gurney and Nisbet (1985) to investigate single-generation cycles. It is thus slightly unusual in having the population control exercised through a food-dependent death rate rather than a food-dependent fecundity. For the Beddington variant of the unstructured model we can show analytically that there is a threshold value of interference above which no possible enrichment of the system can destabilise it.

Many simple predator-prey models predict that sufficient enrichment of a system will drive it into cyclic instability, with further enrichment causing a rapid increase in cycle amplitude to level which, in reality, would lead to extinction of one or both species (Nakajima and de Angelis, 1989). Several authors have tested these predictions but have generally not observed cycles or extinctions as a result of enrichment (McCauley and Murdoch, 1990). We have shown that a small amount of density dependence in the uptake can stabilise our unstructured predator-prey model against unlimited enrichment. This mechanism therefore appears to be a possible candidate explanation for the absence of "paradox of enrichment" effects in natural systems.

Several models in the literature describing a single age-structured species exploiting food supplied at a constant rate exhibit cycles characterised by a period which is slightly greater than the developmental delay and is also comparatively insensitive to all other model parameters: Bellows (1982), Gurney, Nisbet, and Lawton (1983), and Gurney and Nisbet (1985). These "single-generation cycles" can be distinguished from predator-prey cycles, whose period can be strongly influenced by both food and consumer characteristics. Single-generation cycles have previously been observed in host-parasitoid models (Auslander, Oster, and Huffaker, 1974; Godfray and Hassell, 1989; Gordon *et al.*, 1991). We observe both predator-prey and single-generation cycles in our age-structured model, which includes a fully dynamic food source.

In this paper, we show that direct density dependence is even more effective as a suppressor of prey-escape cycles in age-structured models than in their unstructured cousins. However, its effectiveness against single-generation cycles is much weaker, and there are substantial regions of parameter space in which generation cycles are effectively impossible to eliminate. Even where both prey-escape and single-generation cycles can both be stabilised by direct density dependence, the levels required to eliminate

generation cycles are typically an order of magnitude higher than those required to stabilise prey escape cycles.

Direct density dependence can be produced by a very wide variety of mechanisms, including the predator–predator interactions discussed in this paper and the indirect effects of spatial variability (pseudo-interference—Free *et al.*, 1977). Because of the effectiveness of direct density dependence of the type described in this paper in suppressing prey-escape cycles, we should expect the “paradox of enrichment” to be exhibited only by systems from which such interactions are completely absent. However, since single-generation cycles are relatively weakly affected by interference, it seems likely that systems with the dynamics needed to produce such cycles (short adult lifetime, juvenile competition directly expressed in juvenile mortality) will exhibit them even if the predation process exhibits substantial direct density dependence.

Recently, Arditi and co-workers (Arditi and Ginzburg, 1989; Arditi and Akcakaya, 1990) have argued that uptake functions which depend only on the ratio of prey and predator numbers are a more appropriate representation of the process of predation than functions which depend on these quantities separately. Although ratio-dependent predation is heuristically appealing (as well as mathematically convenient) we know of no detailed behavioural model of predation in a homogeneous environment which predicts ratio-dependent uptake over a wide dynamic range of prey and predator populations.

In this context it is worth noting that of the two uptake models considered in this paper, only the Beddington variant has ratio-dependent uptake even as a limiting behaviour. Because Beddington-type behaviour only occurs if predator–predator interactions continue while the participants are feeding, this model predicts that the food standing crop will increase without limit as the system is enriched. Sufficient enrichment will thus always result in a food steady state (F^*) which is large compared to the half-saturation food level (F_0). Equation (18) now shows that in these circumstances the uptake rate is dependent only on the ratio P^*/F^* . By contrast the SIO uptake function, which is derived from the postulate that only searching individuals interact, yields a population model in which food standing crop always goes to a finite asymptotic value as K is increased. However, even if this asymptotic level is large compared to F_0 , the resulting uptake function depends on $P^*/(F^*)^2$ and so is not even approximately ratio dependent.

We are thus forced to the conclusion that under normal field conditions, in which food standing crops tend to be depressed well below carrying capacity, no form of predator interference is likely to lead to even approximately ratio-dependent uptake. This implies that the only mechanisms which might be plausible candidates as a source of true ratio

dependence (*sensu* Arditi) are those which invoke high search rates combined with strong spatial or temporal variability in food availability (Arditi & Ginzburg, 1989). It should be noted however, that most simple versions of such mechanism produce uptake directly proportional to P/F rather than the pseudo-Michaelis-Menten dependence proposed by Arditi *et al.* (1991).

APPENDIX: FUNCTIONAL RESPONSE DERIVATIONS

To analyse the two cases where a searching predator can interact with conspecifics engaged in tasks other than searching we need to redefine W slightly (as the density of interacting individuals who were previously searching) and introduce an extra variable Z ; the density of interacting individuals who were previously handling food. The conservation equation (1) then becomes

$$S + H + W + Z = P. \quad (\text{A1})$$

Case a. Searching Predators Interact with Both Searching and Handling Predators

The reaction scheme for this case is

The dynamic equations for this case are

$$dS/dt = -V_s SF - 2V_s S^2 - V_s SH + W/t_w + H/t_h, \quad (\text{A7})$$

$$dH/dt = -V_s SH - H/t_h + V_s SF + Z/t_w, \quad (\text{A8})$$

$$dW/dt = 2V_s S^2 + V_s SH - W/t_w, \quad (\text{A9})$$

$$dZ/dt = V_s SH - Z/t_w. \quad (\text{A10})$$

From which (using the quantities C and D defined in Eqs. (10) and (11)) we obtain the steady-state solution

$$S^* = [P/4D][-1 + \sqrt{(1 + 8D/(C + 1))}]. \quad (\text{A11})$$

Where $8D \ll C + 1$, this can be approximated by

$$S^* = 1/(C + 1 + 2D), \quad (\text{A12})$$

which yields a functional response

$$I = \max F/(F + F_0 + \sigma P). \quad (\text{A13})$$

Case b. A Searching Predator Interacts Equally with All Other Conspecifics.

Assuming that when a searching predator meets an "interacting" conspecific only the searcher is affected by the collision, the reaction scheme for this case is

The dynamic equations are then

$$dS/dt = -V_s SF - 2V_s S^2 - V_s SH - V_s SW - V_s SZ + H/t_h + W/t_w \quad (\text{A21})$$

$$dH/dt = -V_s SH - H/t_h + V_s SF + Z/t_w \quad (\text{A22})$$

$$dW/dt = -W/t_w + 2V_s S^2 + V_s SH + V_s SW + V_s SZ \quad (\text{A23})$$

$$dZ/dt = -Z/t_w + V_s SH. \quad (\text{A24})$$

The steady-state value of S is

$$S^* = [P/2D][-1 + \sqrt{(1 + 4D/\{1 + C\})}], \quad (\text{A25})$$

which in the weak interference limit ($4D \ll 1 + C$) can be approximated by

$$S^* = P/(1 + C + D). \quad (\text{A26})$$

This leads to a functional response

$$I = I_{\max} F/(F + F_0 + \frac{1}{2}\sigma P). \quad (\text{A27})$$

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