

Why don't predators have positive effects on prey populations?

PETER A. ABRAMS

Department of Ecology, Evolution, and Behavior, University of Minnesota, 318 Church Street S.E. Minneapolis, MN 55455, USA

Summary

Three mechanisms by which increasing predation can increase prey population density are discussed: (1) Additional predation on species which have negative effects on the prey; (2) Predation on consumer species whose relationship with their own prey is characterized by a unimodal prey isocline; (3) Predation on species which adaptively balance predation risk and food intake while foraging. Possible reasons are discussed for the rarity of positive effects in previous predator-manipulation studies; these include the short-term nature of experiments, the large magnitudes of predator density manipulation, and various sources of bias in choice of system and interpretation of results.

Keywords: optimal foraging; predation; predator–prey interactions; mathematical models

Introduction

Predator–prey interactions are commonly defined by one species, the predator, having a negative effect on the population size of the other species (prey), while the prey has a positive effect on the population size of the predator (e.g. May, 1973). In other words, increases in the population size of the predator decrease the population size of the prey, while increases in prey population size increase that of the predator. This definition is found in several textbooks (survey in Abrams, 1987). Even when the predator–prey interaction is defined in terms of effects on population growth rates rather than population sizes, the predator is presumed to have a negative effect on prey population size. In an extensive survey of field experiments on predator–prey systems, Sih *et al.* (1985) found that predator removal (or addition) had the expected positive (or negative) effect on the total abundance of prey populations in all but one of 76 studies in which prey abundance was studied. The one exception (Gilinsky, 1984) was explained (Sih *et al.*, 1985) by the existence of two trophic levels within the prey; predatory bluegills could have a positive net effect on the total insect population by exerting a greater effect on carnivorous insects than herbivorous insects. The absence of significant numbers of cases in which predator addition caused increases in total prey population size did not surprise Sih *et al.* (1985). They state, 'this [lack of positive effects] seems reasonable . . . it is not clear what circumstances would result in predators having an indirect positive effect on total prey abundance.' (Sih *et al.*, 1985, pp. 292–3). Increase in prey density following predator removal or a decrease following predator addition has been seen by some (e.g. Connell, 1975) as one of the most conclusive ways of demonstrating the existence of a presumed predator–prey relationship.

The purpose of this note is to summarize the mechanisms by which increasing predator populations can actually increase the abundance of their prey. The range of possible mechanisms

suggests that such outcomes should not be as rare as they appear to have been in field experiments. Three major classes of mechanisms are discussed: (1) Predation on other predators or competitors of the prey; (2) Predation on a prey whose interaction with its own prey is described by a humped isocline; and (3) Predator-induced reduction of prey foraging, which increases the abundance of the prey's own prey. Possible implications of the rarity of documented positive effects are then discussed.

Mechanisms by which predators can increase prey populations

Virtually all experiments on predation have involved at least semi-controlled changes in predator population density (Sih *et al.*, 1985). The following analysis will therefore treat predator population size as an independent variable. However, the results (aside from possible effects on stability) do not depend on the assumption that predator density is maintained at constant levels by an experimenter. The same effects occur if the predator increases naturally, e.g. because of a decrease in its own death rate. All of the analyses below seek to determine the effect of a change in the predator density (denoted P) on the equilibrium population size of its prey (denoted N).

Mechanism 1: predation on species with negative effects on the prey

It is widely known that predators can have positive effects on the population densities of individual prey species by consuming their competitors or consuming other predators. The review by Sih *et al.* (1985) found that 50% (38 of 76) field manipulations of predator density observed increases in at least one prey. These effects may occur via predation on a competitor; Sih *et al.* (1985) call this the keystone effect after Paine (1966). They may also occur via predation on another predator, which Sih *et al.* refer to as the three-trophic-level effect. The theory behind such positive indirect effects has been investigated in a long series of papers following Levine (1976), and has been summarized by Yodzis (1989).

It seems to be less appreciated (e.g. Sih *et al.*, 1985) that these indirect effects can increase the total density of all of the prey species eaten by a particular predator, as well as increasing the density of individual species. Under the keystone mechanism, increasing predator numbers can increase total prey abundance when a preferred prey species is a superior competitor, but has a relatively low carrying capacity. A positive effect on the set of less-preferred prey (poorer competitors) will occur when the reduction in competition outweighs the increase in predation. A positive effect on the total of all prey occurs whenever this increase is greater than the decrease in abundance of the superior competitor/preferred prey.

Under the three trophic level mechanism, a positive effect on total prey abundance (i.e. first plus second trophic levels) can occur when the top (third level) predator has a sufficiently large capture rate of the second level predator relative to its capture rate of the bottom-level species. The bottom-level increases whenever the decrease in predation caused by a lower density of the second level outweighs the increase in the predation from the third level. The total density of first and second levels increases with an increase in the top predator whenever the bottom level increases by more than the second level decreases.

The verbal descriptions above can be demonstrated by straightforward analysis of the traditional Lotka-Volterra type models (e.g. Pimm, 1982) of food webs and competition. The counterintuitive outcomes described above do not require delicate balancing of parameters, and the conclusions are in no way dependent on any linearity assumptions of these simple models.

Mechanism 2: the prey's relationship with its own prey involves a hump-shaped isocline

Traditional predator-prey theory shows that if: (1) the resource isocline in a consumer-resource system has a unimodal shape; and (2) the consumer isocline crosses the ascending portion of the

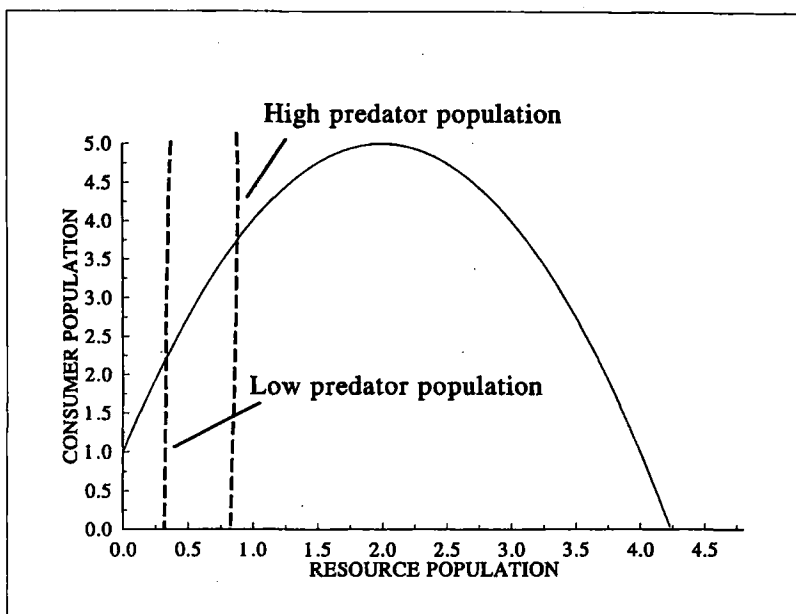


Figure 1. The effect of predator numbers on the isoclines and equilibrium densities in the prey-resource system. Consumer isoclines for two different predator densities are shown. The (unstable) equilibrium consumer density occurs where isoclines intersect.

resource isocline, then increasing the consumer death rate moves the consumer isocline to the right, increasing equilibrium consumer density (e.g. Rosenzweig, 1973). This is illustrated in Fig. 1. A unimodal resource isocline may be produced by a saturating consumer functional response or inverse density dependence in the resource's population growth at low densities (Gilpin, 1975). Clearly, predation is one of the factors that can increase consumer death rate, moving the consumer isocline to the right (Rosenzweig, 1971, 1973; Gilpin, 1975). Thus, if a consumer species has a relationship to its resource that is described by isoclines like those in Fig. 1, an increase in the population of the consumer's predator will increase the equilibrium consumer density.

The system illustrated in Fig. 1 does not have a locally stable equilibrium; predator and prey densities undergo limit cycles. In this case, increasing equilibrium consumer density actually increases the average density during the course of sustained cycles, and reduces the amplitude of the cycles (e.g. Taylor, 1984). If the consumer has a direct negative effect on its own *per capita* population growth rate, its isocline will slope to the right, and a stable equilibrium is possible even though the isoclines cross to the left of the maximum of the resource isocline (Taylor, 1984). Under these circumstances, increasing predation on or harvesting of the consumer, will increase the stable equilibrium abundance of the consumer.

Mechanism 3: the prey exhibits adaptive foraging with a trade-off between food intake and predator avoidance

Most food web models have no explicit consideration of behaviour. One consequence of this assumption is that a prey species' relationship to its resource does not change as the population of its predator changes. This means, for example, that the shape of the resource isocline in Fig. 1 does not change as predator density increases. If, however, the prey adjusts its resource

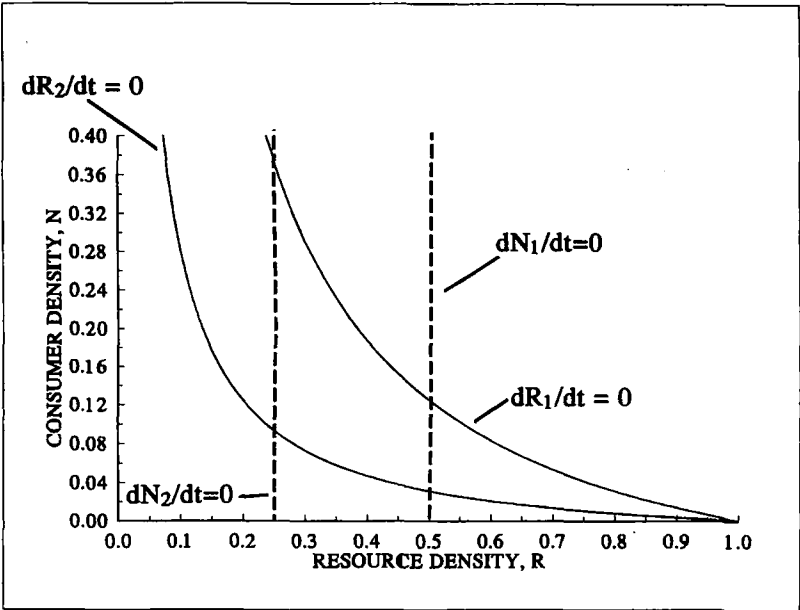


Figure 2. Consumer and resource isoclines for Equation 1 with $g(C) = C^2$, and logistic resource growth ($r = K = 1$). Other parameters are $B = d = 1$. Both isoclines are shown for two different predator densities; isoclines with a subscript 1 are those for $P = 1/16$, and those with subscript 2 are for $P = 1/64$. The equilibrium N (where the isoclines intersect) is $1/8$ for the higher predator density, and $3/32$ for the lower density.

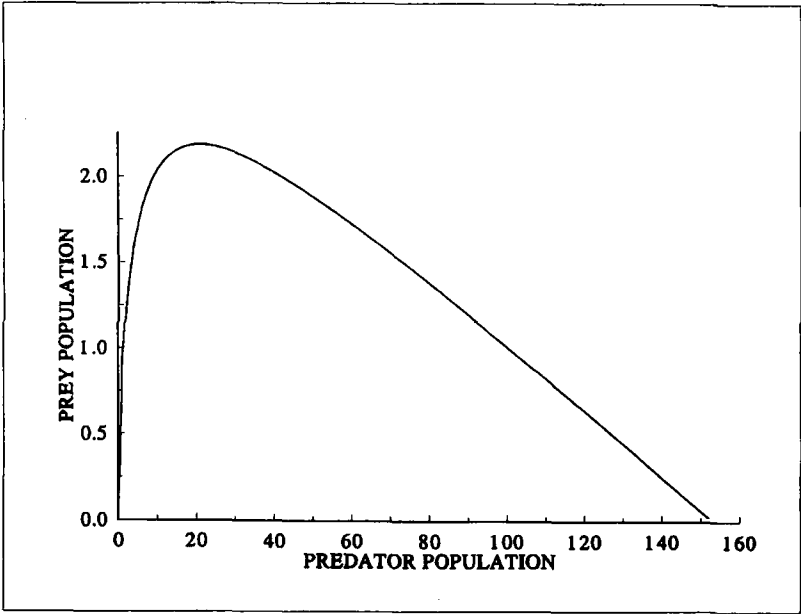


Figure 3. The relationship between equilibrium consumer density and predator density in a system described by Equation 1 with $g(C) = 0.1 + C^2$, and resource growth given by the logistic equation ($r = 1$ and $K = 100$). Other parameters in Equation 1 are $d = 1$ and $B = 1$.

consumption based (in part) on the risk of predation, the shape of the resource isocline will change with predator density. Adaptive consumers forage less when there are more predators (Lima and Dill, 1990; Abrams, 1991); this raises the resource isocline at the same time that the increased predator density shifts the consumer isocline to the right. This is illustrated in Fig. 2, and explained in more detail below. If the rise in the resource isocline is great enough relative to the shift in the consumer isocline, consumer density will increase with increases in the predator population.

Because this type of effect does not occur in the Lotka-Volterra type models of interactions that most ecologists are familiar with, it is useful to present a model which exhibits the effect. A model is also necessary to explain when the shifts in isoclines have the relative values required for prey to increase with predator density. The model is based upon previous analyses of adaptive foraging under risk (Abrams, 1982, 1984, 1987, 1989, 1990, 1991). These analyses assumed that a consumer species must increase its risk of predation if it is to increase its food consumption rate, and that the consumer balances foraging risks and benefits to maximize individual fitness.

The illustrative model assumes that reproduction occurs frequently enough so that individual fitness can be described by the difference between an instantaneous birth rate and an instantaneous death rate (Abrams, 1991). Reproduction by the consumer is assumed to be directly proportional to food intake rate, with a proportionality constant B . Food intake, in turn, is assumed to be the product of foraging effort, C , and food (resource) density, R . The risk per unit time of being captured by a single predator is given by the availability function $g(C)$, which is an increasing function of foraging effort. Phenotypic variability between individuals is assumed to be small enough to neglect. This results in the following model of population dynamics of consumers, N , and resources, R :

$$dN/dt = N[BC_oR - D - g(C_o)P] \quad (1a)$$

$$dR/dt = Rf(R) - C_oNR \quad (1b)$$

$f(R)$ is the function describing resource *per capita* growth rate as a function of its own density. The optimum foraging effort, C_o is given implicitly by the following equation, which determines the C which maximizes both individual fitness and *per capita* population growth of the consumer:

$$BR = g'P \quad (g'' > 0) \quad (2)$$

Primes denote derivatives. See Abrams (1989, 1991) for a more detailed description of this model.

A rigorous analysis of Equations 1 and 2 is presented in section I of the Appendix. The results show that a positive effect of predators on prey occur when; (1) nonforaging individuals of the consumer (N) have an effective refuge from predation; and (2) predator density (P) is below some threshold value. Under these conditions, the rise in the resource isocline increases the consumer equilibrium abundance more than the rightward shift in consumer isocline decreases it. This may also be expressed by saying that, from the standpoint of consumer population growth, the increase in predator density is more than offset by the increase in resource density that occurs when the consumer reduces its foraging. Such overcompensation only occurs when the resource is initially overexploited; i.e. its density is less than that which maximizes resource growth rate (see Appendix). Overexploitation by the consumer will not occur if the initial predator density is sufficiently large. Above a threshold value of P , N decreases with P , resulting in the unimodal N vs P relationship illustrated in Fig. 3.

It is possible to generalize the model described by Equations 1a and b by allowing the relationship between fitness and food intake to be nonlinear; i.e. the reproductive rate is a nondecreasing function $b(CR)$. In general, b levels off (or at least has a negative second

derivative) at high intake rates. The Appendix shows that such a case is even more likely (than Equations 1a and b) to result in a positive relationship between N and P . The intuitive reason is that this case combines mechanisms 2 and 3. When $b'' < 0$, the adaptive variation in C often results in a functional response with a negative second derivative, giving a unimodal consumer isocline (Abrams, 1990). In addition, increased predator density reduces resource exploitation rates, permitting an increase in resource density. Other assumptions of this simple model (Equations 1a and b), such as the additive combination of foraging costs and benefits, can be relaxed without greatly changing the conclusions.

Discussion

There are at least three distinct mechanisms by which increasing the level of predation can result in an increase in the average or equilibrium population size of the consumer. All of the mechanisms involve biological assumptions that seem likely to be satisfied frequently. Mechanism 1 was cited (by Sih *et al.*, 1985) as the probable cause of the positive effects on individual prey species that were observed in one-half of the experimental studies they reviewed. Some conditions must be satisfied for these indirect effects to produce a decrease in total prey abundance. The precise conditions depend on the biological details. However, there does not seem to be any general reason for believing such conditions to be improbable. For example, under the keystone effect, it seems reasonable that a superior interference competitor will often have a lower carrying capacity.

The two conditions that produce hump-shaped consumer isoclines (mechanism 2) are also frequently satisfied. All functional responses must eventually saturate, and Hassell (1978) found that type-two responses were the most commonly observed in laboratory studies. Bianchi *et al.* (1989) argue that positive density effects at low densities are common. Finally, recent work in behavioural ecology has suggested that foragers commonly incur an increased risk of predation while foraging, and behave adaptively with respect to this risk (Godin, 1990; Lima and Dill, 1990).

I know of only one field experiment that could have revealed the type of prey response described by the third mechanism. Turner and Mittelbach (1990) recently analysed the effects of adding predatory large-mouth bass to a system containing bluegill sunfish and their zooplankton and invertebrate resources. This resulted in altered sunfish foraging, significant increases in several bluegill prey species, but no significant change in bluegill population size or mean bluegill body size. However, it did result in a broader distribution of bluegill sizes, which was more skewed to large individuals. This suggests that at least some individuals within the prey (bluegill) population benefited from the predator's presence.

This leads to the question, why are positive effects of predators on the total abundance of their prey apparently so rare (Sih *et al.*, 1985; see introduction of this paper)? Some possible explanations follow:

- (1) Bias in choosing systems for field studies.
- (2) Bias in reporting results.
- (3) Bias in interpreting results.
- (4) Short-term studies do not detect the effects of increased resource densities.
- (5) The assumptions required for the mechanisms are actually rarely satisfied in nature.
- (6) Experiments involve such large increases in predator density and/or harvesting, that positive effects are overwhelmed.
- (7) Typical equilibrium consumer densities are so low that their resources are rarely over-exploited.

It is likely that explanations 1–3 all play some role in reducing the number of reported positive effects of predator on prey. As long as the effect of predators on total prey density is thought to be necessarily negative, positive results will often be attributed to extraneous environmental changes. This can result in failure to publish or failure to interpret results correctly. As Sih *et al.* (1985) note, many manipulative studies do not have sufficient replication because of the amount of effort required for individual replicates. This lack of replicates also makes it more plausible to attribute positive effects to factors other than the manipulated variable (predator numbers). The large amount of work involved in such manipulative experiments may also result in choosing systems for study where there is preliminary evidence of the expected outcome.

Because all three mechanisms discussed here require some form of population response in species other than the prey under consideration (the prey's own food, its predators or its competitors), it is possible that many experiments may be terminated before these responses have occurred. Long term effects from manipulations have been known to be the opposite of short term effects in some systems (e.g. Brown *et al.*, 1986).

I argued above that the conditions required for the three mechanisms are frequently satisfied. However, there have been no surveys of field studies relevant to any of these conditions. We therefore cannot rule out explanation number 5, i.e. that conditions required for these three mechanisms are seldom satisfied.

The sixth argument is that manipulative field studies rarely involve small changes in predator densities. Large changes in conditions are required to achieve statistical significance when the number of replicates is small. Sufficiently large increases in predator density always produce a negative effect on prey under any of the three mechanisms discussed here. It is noteworthy that the study of Gilinsky (1984) found a positive effect of bluegill predation on their prey only in the fall and winter months, when predation levels were relatively low.

The seventh and last explanation listed above is that typically, consumer densities are low enough that their resources are close to their carrying capacities. If true, this would greatly reduce the likelihood that either mechanism 2 or 3 operates. Mechanism 2 would be unlikely because the consumer isocline would cross the resource isocline to the right of its maximum. Mechanism 3 would be unlikely because resources would never be overexploited by consumer species. However, Sih *et al.* (1985) found that predators often reduced prey by a factor of two or more. If this holds true for consumers in general, it argues that many reduce their resources substantially below their carrying capacity in the absence of predators.

Many ecologists would see nothing surprising in the fact that predators have seldom been observed to have a positive effect on the total abundance of their prey. However, given the number and plausibility of the mechanisms that could lead to such positive effects, their absence calls for an explanation. Only future work will reveal whether this absence tells us something about the way nature is organized, or about how previous experiments have been planned and executed.

Acknowledgements

This work was supported by NSF grant BSR 8918646. I thank H. Matsuda and L. Slobodkin for their helpful comments on an earlier draft.

References

- Abrams, P. A. (1982) Functional responses of optimal foragers. *Am. Nat.* **120**, 382–90.
- Abrams, P. A. (1984) Foraging time optimization and interactions in food webs. *Am. Nat.* **124**, 80–96.
- Abrams, P. A. (1987) On classifying interactions between species. *Oecologia* **73**, 272–81.

- Abrams, P. A. (1989) Decreasing functional responses as a result of adaptive consumer behaviour. *Evol. Ecol.* **3**, 95–114.
- Abrams, P. A. (1990) The effects of adaptive behavior on the type-2 functional response. *Ecology* **71**, 877–85.
- Abrams, P. A. (1991) The relationship between food availability and foraging effort: effects of life history and time-scale. *Ecology* **72**, 1242–52.
- Bianchi, T. S., Jones, C. G. and Shachak, M. (1989) Positive feedback of consumer population density on resource supply. *TREE* **4**, 234–8.
- Brown, J. H., Davidson, D. W., Munger, J. C. and Inouye, R. S. (1986) Experimental community ecology: the desert granivore system. In *Community Ecology*. (J. Diamond and T. J. Case, eds), pp. 41–62. Harper and Row, New York.
- Connell, J. H. (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. *Ecology and Evolution of Communities*. (M. L. Cody and J. M. Diamond, eds), pp. 460–90. Belknap Press, Cambridge, Massachusetts, USA.
- Gilinsky, E. (1984) The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* **65**, 455–68.
- Gilpin, M. E. (1975) *Group Selection in Predator-Prey Communities*. Princeton University Press, Princeton, N.J., USA.
- Godin, J. G.-J. (1990) Diet selection under the risk of predation. *Behavioral Mechanisms of Food Selection*. (R. N. Hughes, ed.), pp. 739–70. Springer Verlag, Berlin.
- Hassell, M. P. (1978) *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press, Princeton, N.J., USA.
- Levine, S. (1976) Competitive interactions in ecosystems. *Am. Nat.* **110**, 903–10.
- Lima, S. L. and Dill, L. M. (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–40.
- May, R. M. (1973) *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, N.J., USA.
- Paine, R. T. (1966) Food web complexity and species diversity. *Am. Nat.* **100**, 65–75.
- Pimm, S. (1982) *Food Webs*. Chapman & Hall, New York.
- Rosenzweig, M. L. (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* **171**, 385–7.
- Rosenzweig, M. L. (1973) Evolution of the predator isocline. *Evolution* **27**, 84–94.
- Sih, A., Crowley, P., McPeck, M., Petranka, J. and Strohmeier, K. (1985) Predation, competition, and prey communities: a review of field experiments. *Ann. Rev. Ecol. Syst.* **16**, 269–311.
- Taylor, R. (1984) *Predation*. Chapman & Hall, New York.
- Turner, A. M. and Mittelbach, G. G. (1990) Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* **71**, 2241–54.
- Yodzis, P. (1989) *An Introduction to Theoretical Ecology*. Harper and Row, New York.

Appendix

I. Effect of predator population on prey population based on Equations 1 and 2.

It is clear from Equation 1b that the equilibrium consumer density is given by f/C . Therefore consumer density increases with predator density P provided that

$$Cf\partial R/\partial P - f\partial C/\partial P > 0 \quad (\text{A1})$$

Implicit differentiation of Equation 2 in the text yields an equation for $\partial C/\partial P$:

$$B\partial R/\partial P = g'P\partial C/\partial P + g' \quad (\text{A2})$$

An expression for $\partial R/\partial P$ may be obtained from the condition that $dN/dt = 0$; i.e. $\partial R/\partial P = g/BC$.

Substituting this in Equations A1 and A2, solving Equation A2 for $\partial C/\partial P$ and substituting in A1 yields the following condition for a positive effect of P on N :

$$B(Cg' - g)/(gg''P) > -Cf'/f \quad (A3)$$

A necessary requirement for Inequality A3 to be satisfied is that the left hand side be positive, implying $Cg' > g$. The availability of consumer individuals to their predators, g , can be expressed as the sum of a constant, A_0 , and a nonnegative increasing function $g^*(C)$; A_0 measures the availability of nonforaging individuals to the predators, and g^* measures the increased availability caused by foraging. Because increasing A_0 increases g but not Cg' , a large enough availability of nonforagers makes it impossible to satisfy A3; i.e. larger P cannot increase N .

Given that the necessary condition for positive effects is satisfied (i.e. $Cg' > g$), there exists a threshold value of P , below which Inequality A3 is satisfied. Inequality A3 must be satisfied at small P , because the left hand side of Inequality A3 becomes arbitrarily large as P approaches zero. Further, Inequality A3 cannot be satisfied if P is sufficiently large; this conclusion follows because as N approaches zero, the resource approaches its carrying capacity (f approaches 0), and the right hand side of Inequality A3 becomes arbitrarily large.

Additional insight can be gained by rewriting condition A3 by using Equation 2 in the text to substitute for P , giving:

$$g'(Cg' - g)/Cgg'' > -Rf'/f \quad (A4)$$

The right hand side of Inequality A4 is greater than one if R is greater than the density resulting in maximum resource population growth (i.e. the R which maximizes Rf). The left hand side of Inequality A4 is greater than one if the function g/Cg' increases with C . If g is a simple power function of C (as in Fig. 2), then the left hand side of A4 is always equal to one. Positive effects of P on N will then occur whenever R is overexploited (i.e. is below the density which maximized Rf).

II. Predator effects on prey when prey reproduction is a nonlinear function of food intake rate.

This system differs from Equation 1 in that BCR is replaced by the function $b(CR)$. This changes the equation determining the optimum C to

$$Rb' = g'P (R^2b'' - g''P < 0) \quad (A5)$$

Following the same steps used in deriving Inequality A4 yields the following necessary and sufficient condition for $\partial N/\partial P$ to be positive:

$$[g'(Cg' - g) - (b''gg'CR/b')] / [Cgg'' - (b''gg'CR/b')] > -Rf'/f \quad (A6)$$

If this Inequality is compared to Inequality A4, it differs by the addition of a generally positive term, $-(b''gg'CR/b')$, to both numerator and denominator of the left hand side. (This is positive if $b'' < 0$, which is very likely.) If the left hand side of Inequality A4 is < 1 (this must be true if g is a polynomial with positive coefficients), then Inequality A6 is more likely to be satisfied than is Inequality A4.