A Graphical Solution to a One-Predator, Two-Prey System with Apparent Competition and Mutualism

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ABSTRACT

A system of two noncompeting prey species and one predator is studied, and a graphical method to determine the equilibrium densities of the populations is presented. The method is used to study the behavior of two different systems: with nonterritorial and territorial (self-regulated) predators respectively. It is shown that the introduction of an alternative prey reduces the equilibrium density of the first prey if the predator is not territorial. This is an example of apparent competition. If the predator is self-regulated, then the introduction of an alternative prey may, under some conditions, lead to an increased equilibrium density of the first prey population: apparent mutualism.

1. INTRODUCTION

Coexisting species on the same trophic level may affect one another's population densities in several ways. Interference competition refers to the situation where individuals of one species directly affect individuals of the other species. Interspecific territoriality and interference with each other's foraging behavior are two examples. They are said to exhibit exploitation competition if their main effect on each other is through the utilization of common resources. The classical theory of competing species states that two species cannot coexist unless their resources differ. Much effort has been devoted to the problem of limiting similarity, i.e. how similar the resource utilization of two coexisting species can be. The introduction of predators in such communities leads to another classic problem: Under what circumstances can two species coexist thanks to predation? The possibility of such a diversity enhancing effect was first suggested by Paine [10] and called the problem of competitive coexistence by Vance [14].

However, predation may also affect the coexistence of two species that are not directly competing. If the presence of a prey species increases the density of a joint predator species, this may have an adverse effect on coexisting prey species. This mechanism may lead to competition between

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species that are not directly competing or using common resources. Holt [5, 6] calls this phenomenon apparent competition. He also gives a brief history of the subject and describes field studies which may constitute examples of the phenomenon.

The purpose of this paper is to present a graphic method to compute the equilibrium densities of two "apparently competing" prey species. The method is used to predict circumstances under which a second prey species can be introduced into a one-prey, one-predator system and whether this introduction will increase or decrease the equilibrium density of the first prey species. The scope of the study is limited to systems with populations in equilibrium. Systems with limit cycles or exhibiting "chaos" [7] are not considered.

2. MODELS

2.1. *SYMBOLS*

A	An auxiliary function, related to the combined production rate of two or more prey populations.
a	Defined as r_2/r_1.
b	Defined as K_2/K_1.
C	The consumption rate of a predator population that is in equilibrium with its prey.
F	The feeding rate of predator individuals.
F_{max}	The maximum feeding rate of predator individuals.
F_{min}	The minimum feeding rate of predator individuals.
Fr	A parameter that is related to the shape of the functional response curve.
G, G_1, G_2	The production (growth rate) of prey populations.
i	The point of intersection between A and C.
K, K_1, K_2, K_a	Carrying capacities of the prey populations.
K_p	A parameter that is related to the degree of self-regulation of the predator population.
k_1, k_2	The point of intersection between A and G_1 or G_2.
L	A straight line between i and the origin.
P	Predator density.
r, r_1, r_2, r_a	The intrinsic growth rate of the prey.
r_p	The intrinsic growth rate of the predator.
T, T_1, T_2	The tangent to G (G_1 or G_2) that runs through the origin.
V	Prey (victim) density.
$\hat{V}$	Prey (victim) density at equilibrium.
v, v_1, v_2	The point of intersection between L and G (G_1 or G_2).

2.2. *THE DIFFERENTIAL EQUATIONS*

2.2.1. Different Graphs Used. Two different equations describing the dynamics of the predator and one equation for the prey dynamics are studied. These yield consumption equations and a production equation respectively. A production equation gives the gross production of a prey population at different densities. This dependence was introduced by Armstrong [2]. A consumption equation and the corresponding graph describe the relation between prey density and the total consumption of a predator population that is in equilibrium with such a prey population.

2.2.2. Predator Model I. The predator population is assumed to increase if the prey density is above a particular value. An equation with this property is given by Tanner [13]:

$$\frac{dP}{dt} = r_p P \cdot \left(2 - \frac{F_{\max} - F_{\min}}{F - F_{\min}} \right). \tag{1}$$

The feeding rate F is here, and in all following models, assumed to depend on prey density according to Holling's [4] type II model:

$$F = F_{\max} \frac{V}{\mathrm{Fr} + V} \cdot \tag{2}$$

The consumption graph is a vertical line [Figure 1(a)].

2.2.3. Predator Model II. The second model of predator dynamics pictures a predator with self-regulation, e.g. a territorial species where the size of the territories depends on the realized feeding rate. The predator population never exceeds a density of $K_p \cdot (F_{\max} - F_{\min})$. If the feeding rate is at a certain minimum level or below, the population decreases regardless of present density. Its dynamics is given by

$$\frac{dP}{dt} = r_p P \cdot \left(1 - \frac{P}{K_p \cdot (F - F_{\min})} \right). \tag{3}$$

Assuming that the feeding rate is described by Equation (2), the corresponding consumption graph is [Figure 1(b)]

$$C = \hat{P}\,\mathrm{Fr} = K_p \cdot \left(F_{\max} \frac{V}{\mathrm{Fr} + V} - F_{\min} \right) \left(F_{\max} \frac{V}{\mathrm{Fr} + V} \right). \tag{4}$$

2.2.4. Prey Model. In the absence of predators, the prey populations are assumed to be resource limited. When predators are present, and

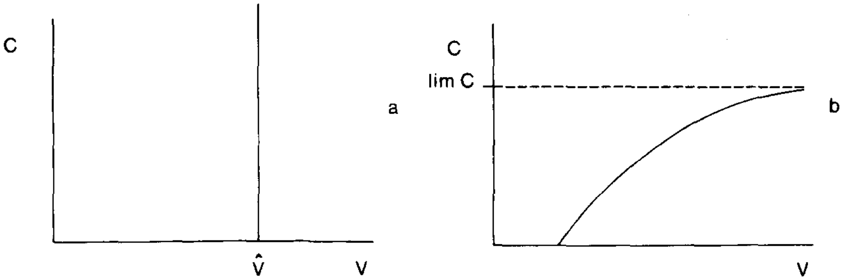


FIG. 1. Consumption graphs: (a) The graph defined in Section 2.2.2:

$$\hat{V} = \mathrm{Fr}\frac{F_{\max} + F_{\min}}{F_{\max} - F_{\min}}.$$

(b) The graph defined by Equation (4):

$$C\left(\frac{\mathrm{Fr}\,F_{\min}}{F_{\max} - F_{\min}}\right) = 0,$$

$$C'\left(\frac{\mathrm{Fr}\,F_{\min}}{F_{\max} - F_{\min}}\right) = \frac{K_p F_{\min}(F_{\max} - F_{\min})^2}{\mathrm{Fr}\,F_{\max}},$$

$$\lim_{V \to \infty} C = K_p F_{\max}(F_{\max} - F_{\min}).$$

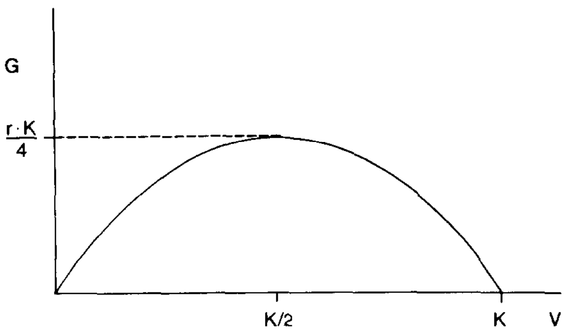


FIG. 2. The production graph: $G'(0) = r$, $G'(K) = -r$.

assuming that predator feeding rate is given by Equation (2), the prey dynamics is described by

$$\frac{dV}{dt} = rV \cdot \left(1 - \frac{V}{K}\right) - PF_{\max} \frac{V}{\mathrm{Fr} + V}. \tag{5}$$

The production graph is given by (Figure 2):

$$G = rV \cdot \left(1 - \frac{V}{K}\right). \tag{6}$$

This is a parabola with V-intercepts 0 and K and with a maximum at $G = rK/4$.

3. A GRAPHICAL SOLUTION OF THE SYSTEM

3.1. *THE TWO-SPECIES SYSTEM*

Intersections between the predator and prey isoclines give equilibrium densities for these populations in the two-species system [11]. However, isoclines cannot be used to solve the three-species system. Equilibria are also given by the intersection between the production and consumption graphs (Figures 1 and 2). On the ordinate the production graph gives the number of prey produced at a particular prey density, while the consumption graph gives the number of prey consumed by a predator population that is in equilibrium with that prey density. The prey population is obviously in equilibrium too at the prey density where the two graphs intersect. Below, a development of the production graph will be used for a solution of the three-species system.

3.2. *THE THREE-SPECIES SYSTEM*

I will now construct an auxiliary graph in the production–consumption-graph diagram. This graph can be used to find the equilibrium densities of two prey populations that are simultaneously exploited by a predator but do not compete directly or for shared resources. This auxiliary graph will, by definition, represent the total growth rate of prey in the system, as a function of total prey numbers. Prey individuals of both species are assumed to be of unit weight, if necessary after adjustment of the K-value. The predator is assumed to consume the prey species in proportion to their respective densities; thus the relation

$$\frac{G_1(\hat{V}_1)}{G_2(\hat{V}_2)} = \frac{\hat{V}_1}{\hat{V}_2} \tag{7}$$

must hold for prey equilibria. This means that there exists a number d such that

$$G_1(V_1) = d \cdot V_1, \tag{8a}$$

$$G_2(V_2) = d \cdot V_2, \tag{8b}$$

and [from Equation (6)]

$$d \cdot V_1 = r_1 V_1 - \frac{r_1 V_1^2}{K_1},$$

$$V_1 = \frac{r_1 - d}{r_1} K_1 \tag{9a}$$

and

$$d \cdot V_2 = r_2 V_2 - \frac{r_2 V_2^2}{K_2},$$

$$V_2 = \frac{r_2 - d}{r_2} K_2. \tag{9b}$$

A is a function of the total prey density V. If V is written as a sum of its component prey densities,

$$V = V_1 + V_2, \tag{10}$$

and if (following the definition above) one requires that $A(V)$ is a prey production consumed by a predator in equilibrium with the two prey species at densities V_1 and V_2 respectively, it is clear that $A(V)$ must be equal to total prey production. Thus

$$A(V_1 + V_2) = G_1(V_1) + G_2(V_2) \tag{11}$$

or [from Equations (7) and (8)]

$$A(V) = d \cdot (V_1 + V_2),$$

$$d = \frac{A(V)}{V}. \tag{12}$$

Equations (9), (10), and (12) give

$$V = \frac{r_1 - \dfrac{A(V)}{V}}{r_1} K_1 + \frac{r_2 - \dfrac{A(V)}{V}}{r_2} K_2,$$

$$A(V) = \frac{r_1 r_2 (K_1 + K_2) V - r_1 r_2 V^2}{r_1 K_2 + r_2 K_1}, \tag{13}$$

the auxiliary function.

3.3. *THE MULTISPECIES SYSTEM*

Equation (9) and the corresponding equations for further prey species can easily be used to deduce equations corresponding to (13). For a one-predator, three-prey system, define

$$V = \sum_{i=1}^{3} V_i. \tag{14}$$

The auxiliary function is given by

$$A(V) = \frac{r_1 r_2 r_3 (K_1 + K_2 + K_3) V - r_1 r_2 r_3 V^2}{r_1 r_2 K_3 + r_1 r_3 K_2 + r_2 r_3 K_1}. \tag{15}$$

3.4. *PROPERTIES OF THE AUXILIARY FUNCTION*

3.4.1. The Auxiliary Graph and Analyses of Predator-Prey Systems. From the definition of the consumption graph, the production graphs, and the auxiliary graphs, one sees how such graphs can be used for a graphical "solution" of a one-predator, multiprey system. Draw a consumption graph, one production graph for each prey in the system, and their ensuing auxiliary graph. Draw a straight line from the intersection between the consumption graph and the auxiliary graph to the origin. The x-coordinates of the intersections between this line and the production graphs represent equilibrium densities of the prey populations.

3.4.2. Extreme Values and Slopes of A. Equation (13) can be rewritten as

$$A(V) = r_a V[1 - V(K_a)], \tag{16}$$

where

$$r_a = \left(\frac{K_2}{K_1 + K_2} \cdot \frac{1}{r_2} + \frac{K_1}{K_1 + K_2} \cdot \frac{1}{r_1} \right)^{-1} \tag{17}$$

and

$$K_a = K_1 + K_2. \tag{18}$$

This is the logistic equation, and it follows that

$$A(V) = 0 \qquad \text{for } V = 0 \text{ and for } V = K_1 + K_2 \tag{19}$$

and that

$$\sup A = \frac{r_1 r_2 (K_1 + K_2)^2}{4(r_1 K_2 + r_2 K_1)}, \tag{20}$$

which is reached for

$$V = \frac{K_1 + K_2}{2}. \tag{21}$$

The slope of $A(V)$ at the origin is given by

$$r_a = A'(0) = \frac{r_1 r_2 (K_1 + K_2)}{r_1 K_2 + r_2 K_1}. \tag{22}$$

As A is an inverted parabola [Equation (13)], we know that [Equation (19)]

$$A'(K_1 + K_2) = -A'(0). \tag{23}$$

Defining $a = r_2 / r_1$, the slope of A at the origin can be written

$$A'(0) = \frac{a r_1^2 (K_1 + K_2)}{r_1 (K_2 + a K_1)} = r_1 a \frac{K_1 + K_2}{a K_1 + K_2}. \tag{24}$$

Because

$$1 < a \frac{K_1 + K_2}{a K_1 + K_2} < a \qquad \text{if} \quad a > 1 \tag{25a}$$

and

$$a < a \frac{K_1 + K_2}{a K_1 + K_2} < 1 \qquad \text{if} \quad a < 1 \tag{25b}$$

and $G'(0) = r$ [from Equation (6)], it is clear that the auxiliary graph runs between the two production graphs in the neighborhood of $V = 0$.

3.4.3. The Tangent to G_2 and K_1 — a Useful Coincidence. The following is a useful property in the analysis of conditions permitting coexistence of prey species. Consider the tangent to G_2 that also passes through the origin. From the fact that $G'(0) = r$ it follows that

$$T_2 = r_2 V. \tag{26}$$

Define $b = K_2 / K_1$. The production graph (G_1), the tangent (T_2), and the auxiliary graph (A) can then be rewritten

$$G_1 = r_1 V \left(1 - \frac{V}{K_1}\right), \tag{27a}$$

$$T_2 = a r_1 V, \tag{27b}$$

$$A = \frac{a r_1^2 K_1 (1 + b) - a r_1^2 V^2}{r_1 K_1 (a + b)} \tag{27c}$$

respectively. Consider the prey density $V^* = K_1(1-a)$. It is easily verified that

$$G_1(V^*) = ar_1K_1(1-a), \tag{28a}$$

$$T_2(V^*) = ar_1K_1(1-a), \tag{28b}$$

$$A(V^*) = ar_1K_1(1-a). \tag{28c}$$

The three graphs thus have a common intersection, the position of which is independent of the ratio between the carrying capacities of the two prey populations, b. This point is k_1 (Figure 3).

3.4.4. r_2, K_2, and the Size of A. Consider r_1 and K_1 given, and study the influence of different values of r_2 and K_2 on the A-graph. a and b are used as relative measures.

From Equation (20) we find the height of A as a function of a and b:

$$(\sup A)(a,b) = \frac{ar_1^2K_1^2(1+b)^2}{4r_1K_1(a+b)} = \frac{ar_1K_1(1+b)^2}{4(a+b)}. \tag{29}$$

If b is kept constant and a $(=r_2/r_1)$ increases from zero to infinity, it is clear from the expression [Equation (29) rewritten]

$$(\sup A)(a) = \frac{a}{a+b}\cdot\frac{r_1K_1}{4}(1+b)^2 \tag{30}$$

that the maximum value of A will increase monotonically from zero to $(r_1K_1/4)(1-b)^2$.

To study the influence of b $(=K_2/K_1)$ when a is kept constant we rewrite Equation (29):

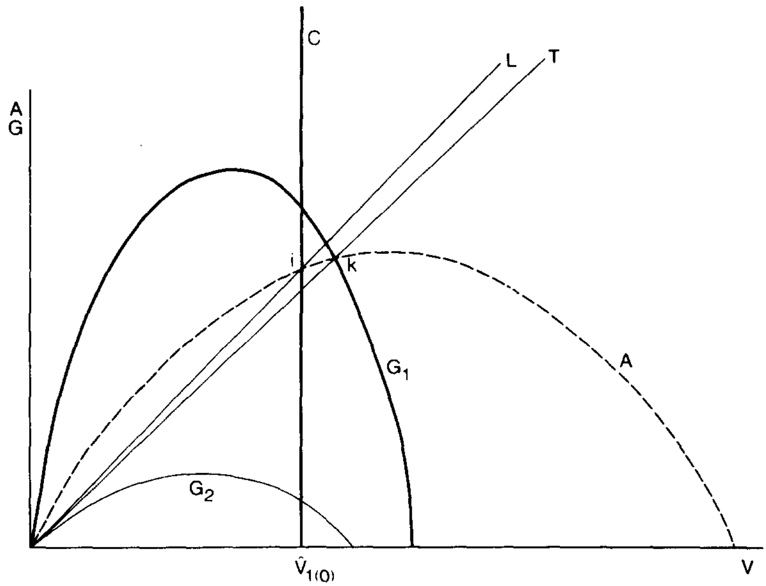
$$(\sup A)(b) = \frac{(b+1)^2}{a+b}\cdot\frac{ar_1K_1}{4}. \tag{31}$$

The derivative of Equation (31),

$$(\sup A)'(b) = \frac{(1+b)\cdot 2(a+1)}{(a+b)}, \tag{32}$$

is positive for all positive (and thus meaningful) values of a and b. Thus $\sup A$ increases with increasing b (K_2).

The width of A is $K_1+K_2 = K_1(1+b)$ [from Equation (19)]. The width of the auxiliary graph is not influenced by a, and it increases monotonically with b.



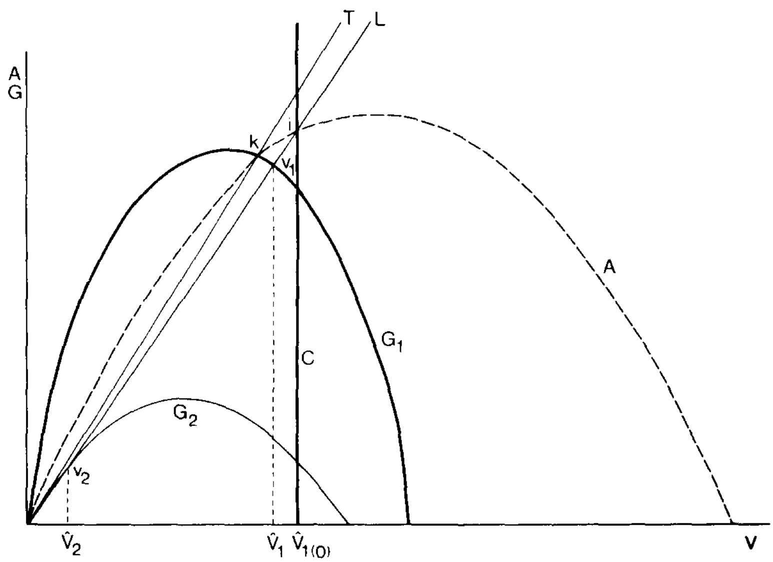


FIG. 3. Graphical analysis of the invadability of a system with one nonterritorial predator and one prey. The consumption graph (C) and the production graph of the first (G_1) and the potentially invading prey (G_2, with tangent T_2) are shown along with the auxiliary graph (A). (a) The line L (from i to the origin) has no positive intersection with G_2, and the second prey cannot invade. (b) A case with a positive intersection between L and G_2. $\hat{V}_1(0)$ represents the equilibrium density of $\hat{V}_1$ in the two-species (one predator-one prey) system. The prey equilibrium densities in the three-species system are $\hat{V}_1$ and $\hat{V}_2$.

4. ON THE POSSIBILITY AND EFFECT OF INTRODUCING A SECOND PREY POPULATION INTO A TWO-SPECIES SYSTEM IN EQUILIBRIUM

Given a production graph G_1 and a consumption graph C, we consider the different effects that are possible on introducing another prey population into this system. The production graph of this new prey population is G_2. For one case (Section 4.1) I discuss the specific effects of characteristics of the second prey species. For the other case (Section 4.2) I only show which qualitatively different cases are possible.

4.1. *A PREDATOR POPULATION WITHOUT INTRASPECIFIC REGULATION*

The consumption graph is a vertical line [Figure 2(a)]. For small values of r_2 (i.e., the alternative prey has a low intrinsic rate of increase), the auxiliary graph will be low [Equation (30)] and the intersection i between C and A will be inside G_1. As the slope of the line from i to the origin (L) is greater than the slope of the tangent to G_2 at the origin (T_2), it is clear that the equilibrium density of the alternative prey population ($\hat{V}_2$) is negative and this prey species cannot invade [Figure 3(a)].

The height of A increases with increasing r_2 [Equation (13)], and for sufficiently large r_2 the point i will be outside G_1. In such cases the slope of L is less than that of T_2. Then the second prey species can invade the community [Figure 3(b)]. It is also clear that the equilibrium density of the first prey population will be less after the introduction of a second prey species ($\hat{V}_1$) than it was before such an invasion ($\hat{V}_{1(0)}$) [Figure 3(b)].

An increase in K_2 (increasing b) increases both the height and the width of the auxiliary graph. Therefore the effect of this parameter of the invading properties of the alternative prey is less clear. Depending on the value of a, an increase in b may either increase ($a > 1$) or decrease ($a < 1$) the slope of the auxiliary graph at the origin [Equation (24)] and thus the y-coordinate of i and the slope of L. The slope of T_2 is r_2 and remains unaffected by changes in K_2. It thus follows that, depending on other variables, an increase in K_2 may or may not increase the invading capacity of the alternative prey species.

4.2. *A PREDATOR POPULATION WITH INTRASPECIFIC REGULATION*

The consumption graph of a predator population with intraspecific population regulation starts with a relatively steep slope and levels off. If the slope is sufficiently steep and the V-intercept sufficiently low [a predator with weak regulation that is efficient (survives on low prey densities)], the point i may be inside the G_1-graph and thus the slope of L steeper than that of T_2 [Figure 4(a)]. This means that the second prey population cannot

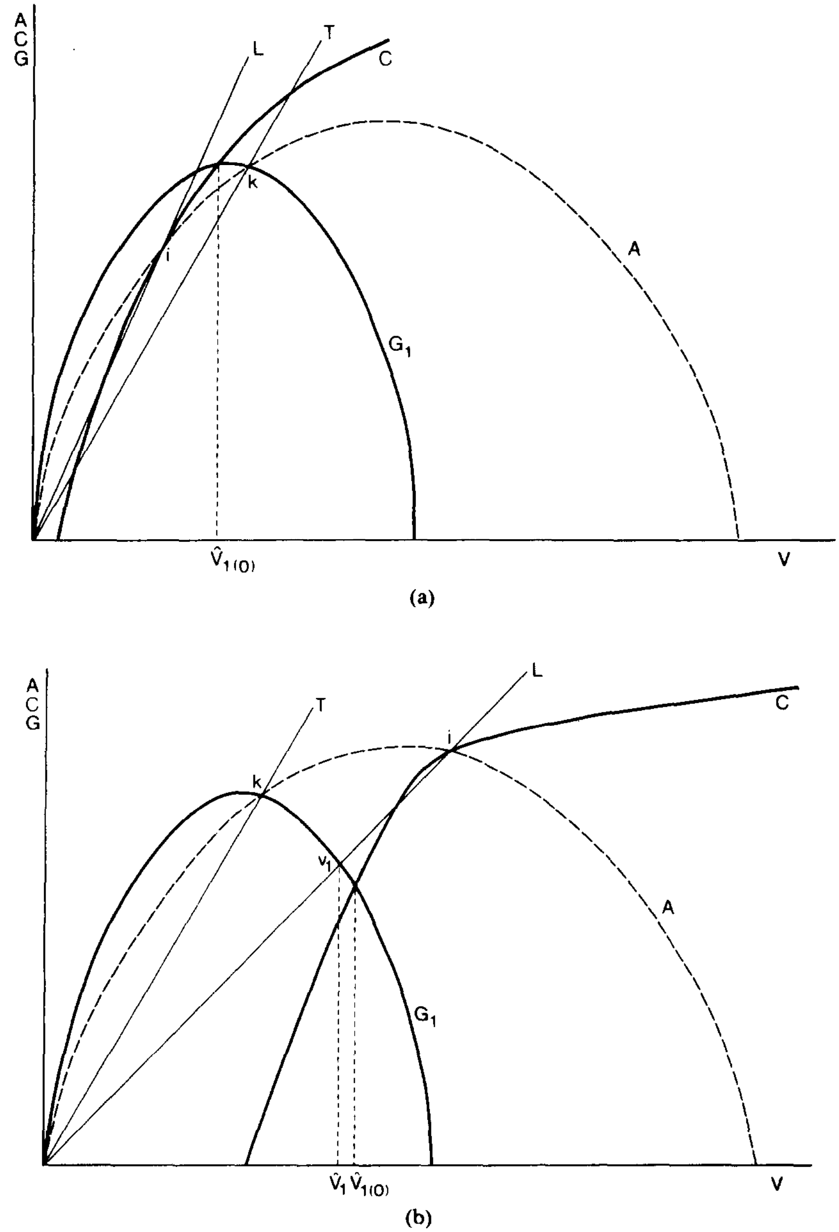
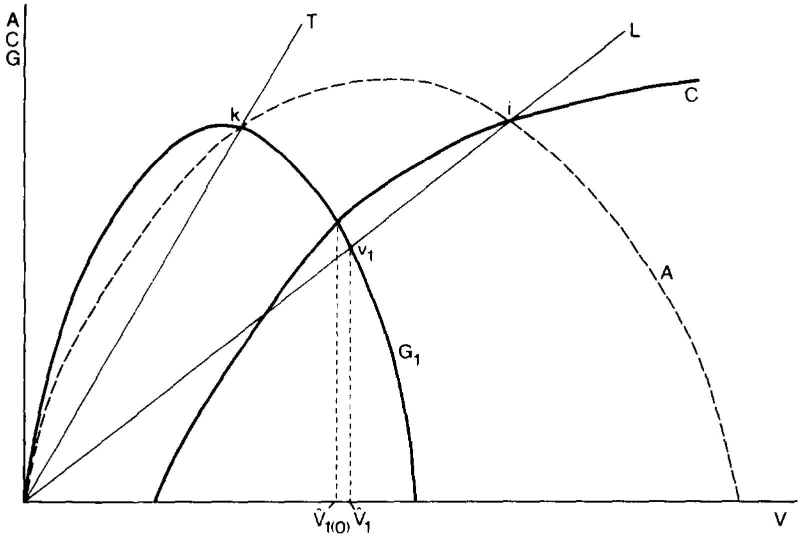


FIG. 4. Graphical analysis of the invadability of a system with one territorial predator and one prey. Abbreviations as in Figure 3. (a) A case where the potential second prey species cannot invade. (b) A case where the potential second prey species can invade, resulting in the reduction of the equilibrium density of the first prey species. (c) A case where the potential second prey species can invade, resulting in the increase of the equilibrium density of the first prey species.



(c)

FIG. 4. *(Continued)*

invade the system. With other characteristics of the C-graph, the second prey may invade the system [Figure 4(b) and (c)]. The density of the first prey may, as for a nonterritorial predator, decrease [Figure 4(b)] or increase [Figure 4(c)].

4.3. *PREDATOR CHARACTERISTICS AND PREY-SPECIES DIVERSITY*

The following characteristics of the predator population will push the point i to the right and thus give L a slope that is more likely to be less than T_2. This will facilitate the invasion of a second prey species:

(1) A low feeding rate at low prey densities [high Fr, Equation (2), Figure 5(a) and (b)].

(2) Strong intraspecific predator regulation [low K_p, Equation (3), Figure 5(b)].

(3) A low maximum feeding rate of the predator [low F_{max}, Equations (2a) and (4), Figure 5(a) and (b)].

(4) A high minimum feeding rate [high F_{min}, Equations (2) and (4), Figure 5(a) and (b)].

Diversity is thus promoted by characteristics that reduce the overall effect of predation.

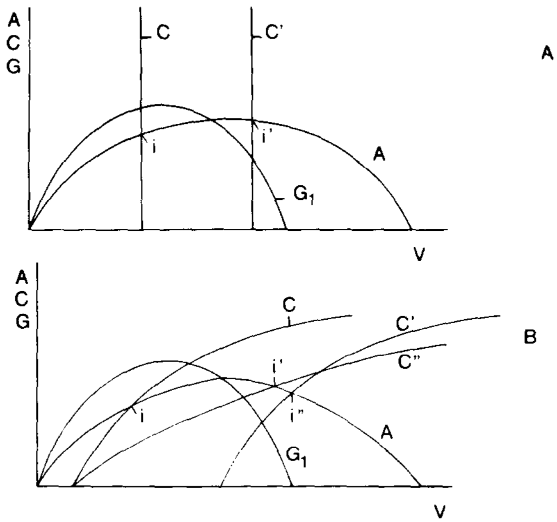


FIG. 5. Changes in the parameter values of the C-graph that increase the possibility for the alternative prey to invade a two-species system. C represents a condition where V_2 is less likely to invade than do C' and C''. (a) A nonterritorial predator. High values of Fr and F_{min}, and a low value of F_{max}, lead to C'. (b) A territorial predator. A low value of K_p leads to C'. High values of Fr and F_{min}, and a low value of F_{max}, lead to C''.

5. DISCUSSION

5.1. *GRAPHICAL METHODS*

Previous graphical analyses of predator-prey interactions have been based on, e.g., isoclines [1, 9] or production curves and functional response curves [2]. These analyses have usually focused on stability conditions [11, 2, 12] or on conditions affecting the coexistence of prey species [3, 9]. In the present paper I introduce the consumption graph, which is particularily adapted to analyse quantitative effects on the equilibrium densities of multiprey communities with a shared predator. Similar effects are also discussed qualitatively by Abrams [1]. However, he does not adapt his graphical method for the explicit prediction of equilibrium densities; it is used to predict the direction of changes.

5.2. *APPARENT COMPETITION AND COOPERATION*

The densities of two prey populations at equilibrium that are preyed upon by the same predator are usually less than those of a prey population that is the sole prey species in the system. This is also the general conclusion drawn by Holt [5], which led him to coin the term apparent competition. The phenomenon has in recent years been discussed again by Holt [6] and by Mithen and Lawton [8]. In addition to the mutual negative effect discussed by these authors, the analysis above demonstrates that the introduction of an alternative prey species may lead to an increase in the density of the first prey. Such situations may arise if the predator is self-regulated (e.g. territorial). Holt [5] mentioned the possibility of such effects if a higher-order predator is included in the system. He labeled such situations apparent mutualism. Conclusions similar to mine were reached by Abrams [1], partly on the basis of results from Noi-Meir [9], by means of another graphical method.

The notion of apparent mutualism thus seems to be theoretically acceptable. However, I presently do not know of any field studies that are convincing evidence of its existence. The mechanism may have some relevance for the management of natural populations. If, e.g., one wants to increase the size of a population that is limited by predation, introduction of an alternative prey will in the short run ("behavioral time") do this. In the long run ("ecological time"), the action is most likely to be successful if the predator is territorial.

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