



## Graphical Representation and Stability Conditions of Predator-Prey Interactions

M. L. Rosenzweig; R. H. MacArthur

*American Naturalist*, Vol. 97, No. 895 (Jul. - Aug., 1963), 209-223.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28196307%2F08%2997%3A895%3C209%3AGRASCO%3E2.0.CO%3B2-L>

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

*American Naturalist* is published by The University of Chicago Press. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

---

*American Naturalist*

©1963 The University of Chicago Press

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact [jstor-info@umich.edu](mailto:jstor-info@umich.edu).

©2003 JSTOR

GRAPHICAL REPRESENTATION AND STABILITY CONDITIONS  
OF PREDATOR-PREY INTERACTIONS

M. L. ROSENZWEIG AND R. H. MACARTHUR

Department of Zoology, University of Pennsylvania, Philadelphia, Pennsylvania

## INTRODUCTION

Investigators have employed two major pathways when inquiring into the nature of the predator-prey interaction. One of these has been to disassemble the interaction into as many component parts as possible and then characterize these for various specific predator-prey relationships. This approach is certainly necessary to a complete understanding of any given predator-prey interaction, but it does not stress, nor has it been fruitful at the task of making general statements about two central ecological problems. Does the interaction contribute to the observed stability of natural communities? In what direction, towards or away from a stable interaction, does the force of Natural Selection drive the predator and its prey? We shall herein embark on the second pathway, that of generalization, and attempt to begin to answer these two questions.

## THE GRAPHICAL DESCRIPTION

One of the most common relationships between two populations involves the destruction by members of one population of members of the other for the purpose of obtaining food. This predator-prey relationship is marked by a mutual interaction of the two populations involved. To examine this interaction, let us make a graph with predator density as ordinate and prey density as abscissa. Each point on the graph will then represent a unique community composition; that is, prey at density  $x$ , predators at density  $y$ . Let us postulate that by ascertaining the community composition, we can unambiguously state the instantaneous rate of change of both the predator's and the prey's density.

Parenthetically speaking, this uniqueness is not absolutely true, as populations of identical density might differ in other characteristics which we do not show on the graph—and which are therefore items being held constant for the sake of the argument. Such characteristics as are probably important are average reproductive value (see Slobodkin, 1961), adrenal function (see Christian, 1961) and, undoubtedly, a host of other important items both discovered and awaiting discovery. This oversimplification, however, will not affect the qualitative outgrowths of the argument.

Let us now suppose that we run countless experiments by starting a predator-prey community at many different community compositions in identical environments, and recording whether the prey increased, decreased, or just maintained itself, and also noting the same information for the predator.

We plot all of the above data on our graph by inserting two arrows at each of the community composition points that we have tested. One arrow will be parallel to the x axis and will show us the magnitude and direction of change of the prey (toward y axis equals decrease; away from it equals increase; no arrow equals no change). The other arrow will be parallel to the y axis and will do the same for the predator.

Now we connect all the points at which the prey population just maintained itself, and call the resulting line the prey isocline ( $\frac{d \text{ Prey}}{dt} = 0$  for all points on the line). Let us also connect the points at which the predator population just maintained itself and call this the predator isocline. If the lines intersect, neither population will be changing at the point of intersection. Such points, if any exist, are called the equilibrium points of the interaction.

Now we can proceed with a deduction of the general shape of each of the two isoclines, and from them make deductions about the stability of the interaction. Each population possesses a set of just-maintainable densities,  $\frac{d \text{ pop.}}{dt} = 0$ , for otherwise a population would be increasing or decreasing ad infinitum. If decreasing, we wouldn't observe it (it would be extinct); if increasing, it would eventually contradict the first law of thermodynamics. When a population is not at one of its just-maintainable densities, it is either increasing or decreasing. Also, in a continuous model, a population cannot pass from an increasing state to a decreasing one, or vice-versa, without attaining an equilibrium point en route.

We shall start with mental construction of the prey isocline to determine its general shape. First, consider what point(s) will result in the prey species just maintaining itself when there are no predators. Clearly, there will be a minimum just-maintainable density of prey associated with the minimum density of the prey species required for successful one-for-one reproduction; call this the minimum just-maintainable density,  $P_0$ , for the prey population with no predators. Also, there will be a point,  $Q_0$ , a maximum just-maintainable density for a prey population with no predators. Beyond this, the prey will be overcrowded; after all, the prey itself, since it is also animate, will depend on some limited source of life, be it solar energy, grass, or simple space. In experiments whose initial populations are represented by any point on the line between  $(P_0, 0)$  and  $(Q_0, 0)$ , the prey will begin by increasing; at an initial point on the line to the left of  $(P_0, 0)$ , it will decrease to extinction; at an initial point to the right of  $(Q_0, 0)$ , it will begin by decreasing.

Assume the predators are able to eat the prey at every prey density between  $P_0$  and  $Q_0$ . If we take a prey density,  $x$ , and hold it constant in a series of experiments like those previously outlined, the prey will begin by maintaining themselves or increasing if and only if the predators begin at or below a certain density. If the predators begin at too high a density, the

prey population will begin by decreasing. This means that over every prey density between  $P_0$  and  $Q_0$ , there exists a population composition at which the prey just maintain themselves. The set of all population compositions for which the prey just maintain themselves is thus a closed curve, such as that for  $\frac{dPy}{dt} = 0$  in figure 1.

To prove that this curve is of a form similar to that in figure 1, that is, that it has one and only one peak, let us examine the interaction for constant predator densities and vary the prey. We add several members,  $i$ , of a

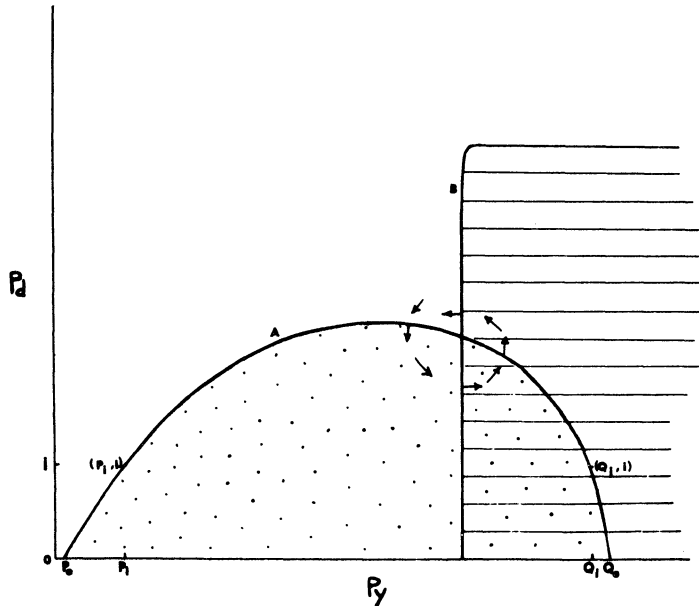


FIGURE 1. The instantaneous model of the interaction of a food-limited predator and its prey.  $P_y$  = prey density;  $P_d$  = predator density. Line A is the prey isocline, that is, the set of all points for which  $\frac{dPy}{dt} = 0$ ; line B is the predator isocline.  $P_y$  increases in the dotted area only;  $P_d$  increases only in the shaded area. The vectors are the instantaneous (general) direction of change of the community at eight qualitatively-different points in the graph.

species of predator (which preys exclusively on our first species). These predators are living ultimately on the same resources as their prey. Since the prey's biomass can be limited by its own resources, then the additional onus on the resources (caused by the maintenance of the predator biomass), results in a decrease in the amount of prey biomass that can be maintained. Slobodkin (1962) has shown in superb laboratory studies that the amount of the "standing crop" of a *Daphnia* population which is limited by its resources is indeed decreased by the presence of predation. The maximum just-maintainable density,  $Q_1$ , at this population of predators,  $i$ , will thus usually be less than  $Q_0$ ; it certainly can be no greater. On the other hand, due to the fact that the prey are being eaten, more prey will be necessary

for successful one-for-one replacement of the prey population; that is,  $P_i > P_0$ . The prey will begin by increasing in experiments whose initial populations are represented by points on the horizontal line between  $(P_i, i)$  and  $(Q_i, i)$ , and by decreasing at points on the line to the right of  $(Q_i, i)$ . At initial points to the left of  $(P_i, i)$ , the prey will no longer of necessity become extinct (although they will begin by decreasing), for the predators, too, may well be growing scarcer. A continuation of this type of reasoning leads to the inevitable conclusion that as we add more of the predators to the initial community, the minimum just-maintainable density increases and the maximum just-maintainable density decreases. The form of the prey isocline is thus confirmed to be the form of the curve in figure 1. The dotted area is the set of all points (population compositions) at which the prey are increasing; in the undotted area are all the points at which the prey are decreasing.

At  $(Q_0, 0)$  when there are no predators, the prey are limited by their own resources; at  $(P_0, 0)$  they are limited by their own reproductive ability. Increasing the numbers of predators in the community decreases the reproductive efficiency of the prey, and the amount of prey maintainable on the limited resource(s). As we pass from left to right, interference with reproduction becomes less important as a prey-limiting factor, and drain on prey resources becomes more important. Obviously, the slope of the isocline or its exact shape is not the same for every predator-prey relationship.

The predator isocline,  $\frac{dPd}{dt} = 0$ , is simpler to deduce. The predator is depending on the prey for its ability to increase. When the prey fall below a certain level, the predators decrease; when they are greater than this level, the predators increase. Since we are dealing with an instantaneous model, the predators will be increasing if and only if they are eating prey at the required rate (Andrewartha and Browning, 1961). Attainment of this rate depends only on the prey density. It is true that the greater the number of predators, the faster the 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. This results in the vertical line segment of  $\frac{dPd}{dt} = 0$  in figure 1; that is, the predators increase if and only if the prey exist at or above a certain density. The shaded area is the region of predator increase; the unshaded area is the region of predator decrease. With vertebrate (and some other) predators, where increase is discontinuous and depends, in part, on accumulated food intake, greater densities of predators do indeed require greater densities of prey for increase. This model introduces a positive slope to the predator isocline (see lower part of  $\frac{dPd}{dt} = 0$  in figure 3); that is, at greater predator densities, greater prey densities are required for predator increase.

The predator has other limitations (for example, standing room) besides food which he must eventually reach, and beyond which he may not increase, no matter what extravagant density the prey population might attain. This fact places a "ceiling" (the horizontal part of  $\frac{dPd}{dt} = 0$ ) on the predator's ability to increase, as in figures 1, 3, and 4.

Figure 1 gives us the instantaneous model of predator-prey interactions for a food-limited predator. Addition of the component population vectors to obtain the resultant community vectors at eight points in the graph demonstrates the nature of the community vectors in each of the graph's eight divisions. A community history is graphed by observing the numbers of the two populations at different times, and placing them as points on our graph. Due to the general direction of the community vectors in each of the eight "locations," we can predict that this history, if plotted on a graph like figure 1, might result in the arrow's forming an elliptic curve, that is, given a starting point, the community composition would return to a point at or near this starting point. If the community did not return to the precise point, then the vectors would describe a spiral with either inward (stable) or outward (unstable) flow. If the spiral ever got so large that one of the axes were intersected by a vector, the predators (in case of intersection with x axis) or both species (in case of intersection with y axis) would become extinct. Graphing the points of such spirals with predator and prey on the ordinate and time on the abscissa will demonstrate the fact that these spirals are just a different way of graphing "classical" predator-prey oscillations (see Huffaker, 1958, and Utida, 1957).

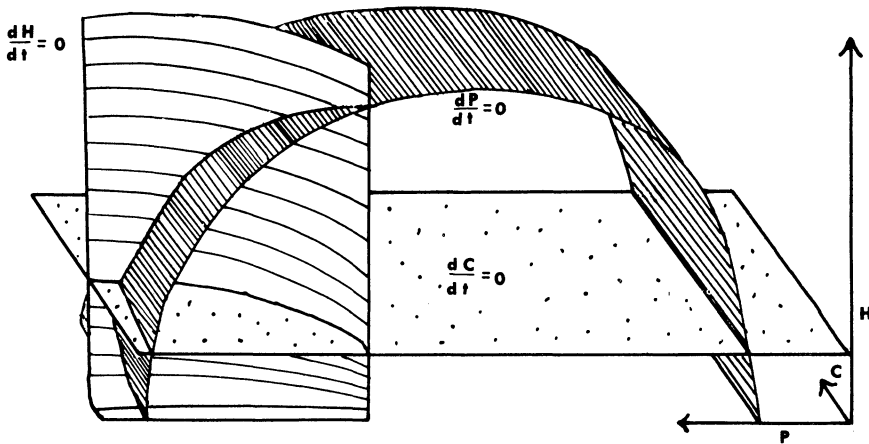


FIGURE 2. The interaction of a carnivore (C), and herbivore (H), and a plant (P). Dotted and shaded areas are the isosurfaces as marked. The plants increase their density at every point below the "airplane hangar" surface; the herbivores increase theirs at every point on the observer's side and to the left of their isosurface; the carnivores increase theirs at all points above their planar isosurface. Vectors, though applicable, are omitted for the sake of clarity.

As we shall later demonstrate, such spirals are not a necessary feature of every interaction. Some isoclines are so formed that both predator and prey approach an equilibrium value (be it zero or positive) asymptotically.

Graphical description of predation can readily be extended to the three species interaction. An interesting example of this is a graph (in three dimensions) of a carnivore eating an herbivore which is eating a plant. Figure 2 is a picture of such a graph. Dotted and shaded areas in this case are not regions of increase or decrease, but are the isosurfaces of the species involved. The present investigators are attempting analysis of such interactions similar to the one for two dimensions which follows below. Four-dimensional situations are unfortunately beyond our collective imagination, but it is hoped that analysis of the three-dimensional models and comparison with the two-dimensional ones will reveal trends which can be tested in the laboratory and the field.

#### VARIATIONS OF THE MODEL RESULTING IN GLOBAL STABILITY

A basic premise of all of these arguments has been that the rate of predation varies proportionately with the prey density. Holling (1957) has found at least one example, however, where increasing prey density has no effect on predation rate. Can our graphical system handle this instance?

Since the predation rate is constant at any level of prey density, the predator increases or decreases without regard to the prey density. It is thus limited by something other than prey density. This is the meaning of the horizontal segment of our isocline, and if such a situation pertains at the interaction equilibrium point, we may graph it by lowering our "ceiling" as

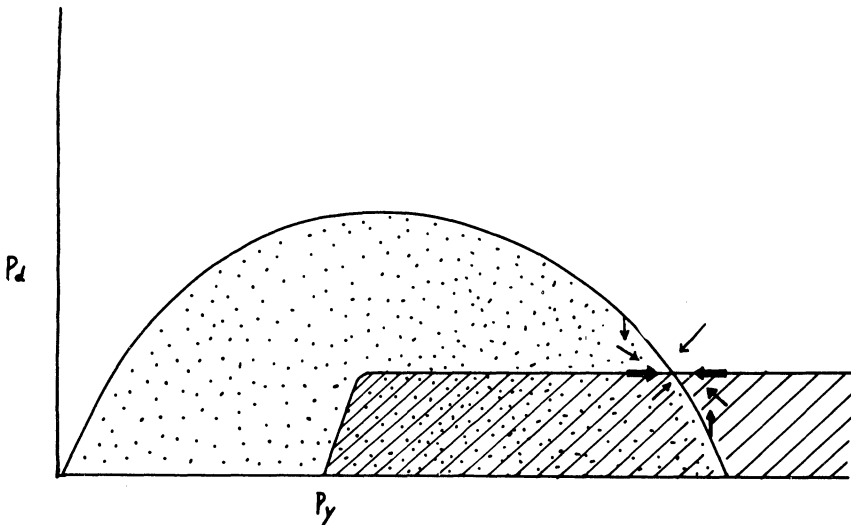


FIGURE 3. The interaction of a predator and its prey, where the predator is not limited at its equilibrium density by its supply of prey. Isoclines, coordinates, and markings as in figure 1. Vector construction demonstrates that oscillations are not present, but that a stable equilibrium is.

in figure 3. Vector construction in this case shows us that we have a stable equilibrium with no oscillations. Such stability, over the whole area of the graph will be termed global stability.

Since both figures 1 and 3 may well describe the incomplete utilization of a resource, we have a good reason for suspecting that each is perhaps modified towards figure 4, which represents a predator limited by more than one of his resources. For instance, a predator that is not food-limited is permitting waste on his trophic level. This provides an opportunity for some other predator to move in and "take up the slack," causing the density of food to become more important to our original predator. If the second predator takes up all the slack, superficially one obtains exactly figure 4; however, due to the variation of a second predator, we must add it on a third axis. Such multi-dimensional cases will be discussed later.

Similarly, a strictly food-limited predator is not utilizing some other feature of his "niche" to its utmost, a situation representable by figure 1. Addition of another species to utilize the wasted resource (for example, space) results in a lowering of the "ceiling" of the predator. This phenomenon seems intuitively less potent than the maximization of food consumption discussed above. Either force might also be channeled into a "ballooning" of the single predator "niche" as observed in Bermuda by Crowell (1960). The net effect of this "nature abhors a vacuum" idea is

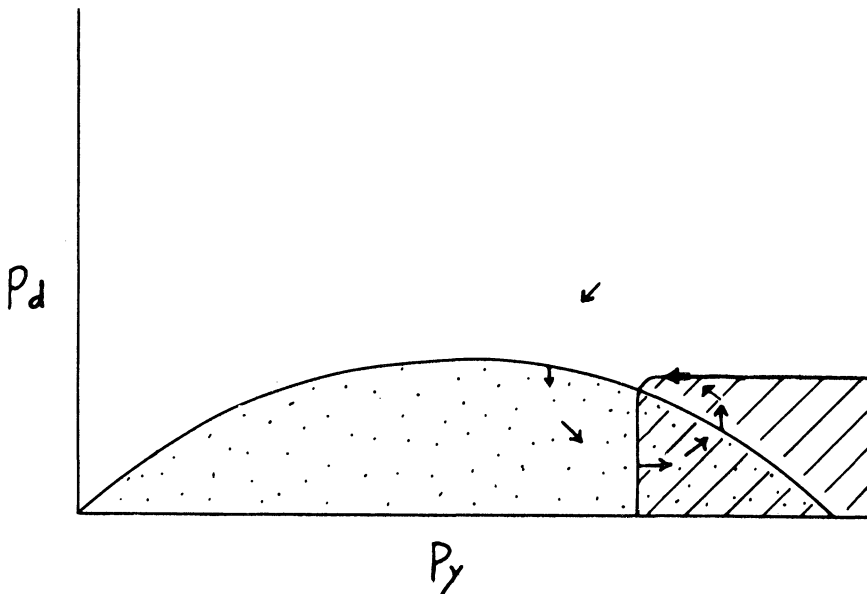


FIGURE 4. The interaction of a predator and its prey where the predator is limited at its equilibrium density both by its supply of prey and some other resource(s), for example, nesting sites or den space. Isoclines, coordinates, and markings as in figure 1. Vector construction demonstrates the fact that oscillations take place only in the extremely small area close to equilibrium, where they are probably unmeasurable.



the simultaneous limitation of the predator by all the resources of its environment (figure 4).

Vector construction in figure 4 shows how the horizontal segment of the predator's isocline causes a funnelling of the community vectors into interaction equilibrium. The limitation of the predator by multiple factors thus means that oscillations can take place only in the very small area around interaction equilibrium where the predator isocline is not horizontal. There they would probably be of undetectably small magnitude.

Another assumption we may negate with profit is that the predators are able to eat prey at any prey density between  $P_0$  and  $Q_0$ . If we assume instead that the prey have some inviolable haven able to support a certain density of prey completely free of predation, then we get an open curve like that in figure 5. Vector construction in this system shows that because the community actually travels along the prey isocline when it is vertical, any series of community oscillations must eventually attain a maximum where one of the points reached is the point at which the prey isocline first begins to slope.

The only other line segment that remains, that is, the right side of the prey isocline, can also become vertical when there is no predation pressure at high prey and moderate predator densities. When this occurs, a maximum oscillation is similarly created. The community travels up along the isocline until it reaches the point where the isocline slopes. Therefore,

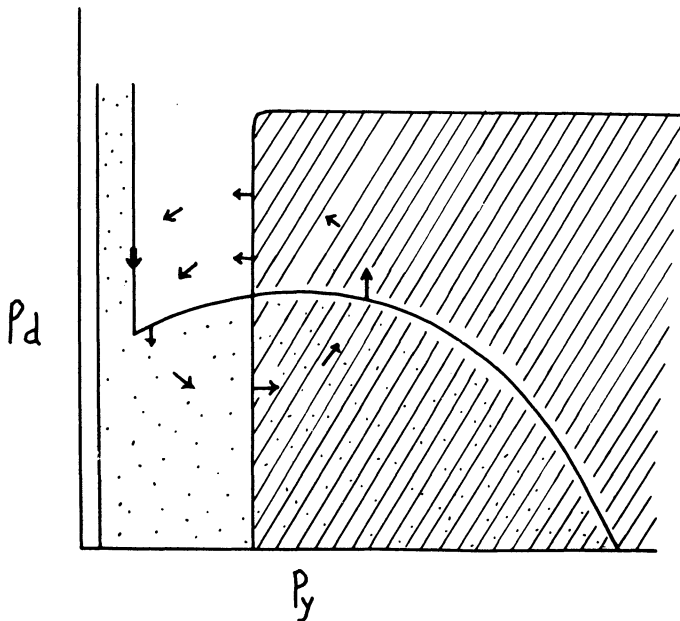


FIGURE 5. The interaction of a predator and its prey where the predator is unable to eat the prey at every prey density. Isoclines, coordinates, and markings as in figure 1. In this case, growing oscillations do not necessarily grow until one or both species becomes extinct, for a limiting oscillation may be reached.

this point will be reached in every oscillation after it is first reached, and we may describe the unique limiting oscillation by starting the community at this point and reporting its numbers until it returns there.

We do not mean to imply the necessity of a non-extinguishing oscillation, given either the "prey-hideaway" isocline or the "no-predation-pressure-at-moderate-predator-levels" isocline. The maximum oscillation may intersect one of the axes, in which case one or both species would become extinct (perhaps even before the maximum oscillation were attained). We suggest these isoclines merely as a possible means of control of some predator-prey oscillations. Their control will be exercised if and only if the oscillation is unstable close to community equilibrium, and the maximum oscillation intersects neither axis. All of these remarks apply equally well to the horizontal "ceiling" isocline of the predator, which isocline is also capable of limiting the oscillatory amplitude by inducing a maximum oscillation.

STABILITY OF LINEAR APPROXIMATION

A general theory of global stability of the food-limited predator's interaction with his prey is difficult to attain. Let us instead consider a lesser topic: stability of a linear approximation close to the interaction equilibrium point. Determination of this will at least enable us to answer the question: What are the graphical conditions which result in appearance of predator-prey oscillations? Regular oscillations should occur if the system is unstable at equilibrium (that is, the small oscillations are of increasing amplitude), but globally-stable. Recognizable oscillations of predictable period and large amplitude probably do not occur where the system is stable at community equilibrium (that is, the oscillations are of decreasing amplitude) and the natural complex of weather factors and chance is present.

Transposing the origin of our axes to community equilibrium, we note that new values for the abscissa are  $x = py$  minus  $py_{eq}$ , and for the ordinate  $y = pd$  minus  $pd_{eq}$ . At community equilibrium,  $x = 0$  and  $y = 0$ . Here the rate of increase of the prey at any point is directly proportional to the distance down from the prey isocline (whose equation is approximately  $y = k_1x$ ), and the rate of increase of the predator at that point is directly proportional to its distance in the positive direction from the predator isocline (whose equation is approximately  $y = k_2x$ , or when  $k_2$  does not exist,  $x = 0$ ). We can thus write differential approximations as follows:

$$(1) \quad \frac{dx}{dt} = a(k_1x - y)$$

$$(2a) \quad \frac{dy}{dt} = \beta \left( x - \frac{y}{k_2} \right),$$

or when there is no slope (pd isocline has equation,  $x$  equals zero):

$$(2b) \quad \frac{dy}{dt} = \beta x.$$

$\alpha$  and  $\beta$  are positive constants involving the Malthusian parameters of the prey and the predator respectively.  $\alpha$  is the change in  $dx/dt$  accompanying a unit change in the predator population.  $\beta$  is the change in  $dy/dt$  accompanying a unit change in the prey population.

Let us try to analyze situation (1) and (2b) where the predator's rate of increase is independent of his own density. We shall try to find a common parameter for the two populations,  $m$ . Since these are linear differential equations, we should be able to express their solutions as exponential functions:

$$(3a) \quad x = Ae^{mt}, \quad (3b) \quad \frac{dx}{dt} = mAe^{mt} = mx = \alpha(k_1x - y).$$

$$(4a) \quad y = Be^{mt}, \quad (4b) \quad \frac{dy}{dt} = mBe^{mt} = my = \beta x.$$

Using (4b), we obtain:

$$(5) \quad y = \beta x/m, \text{ which upon substitution into (3b) yields}$$

$$(6) \quad mx = \alpha(k_1x - \beta x/m) \quad \text{or} \quad x[m^2 - (\alpha k_1)m + \alpha\beta] = 0.$$

Since we are not interested in the root,  $x = 0$ , of this equation (prey are at equilibrium and will by definition stay there), we eliminate it. We can thus solve for  $m$  in the usual way, obtaining

$$(7) \quad m = \frac{\alpha k_1}{2} \pm \frac{\sqrt{\alpha^2 k_1^2 - 4\alpha\beta}}{2}.$$

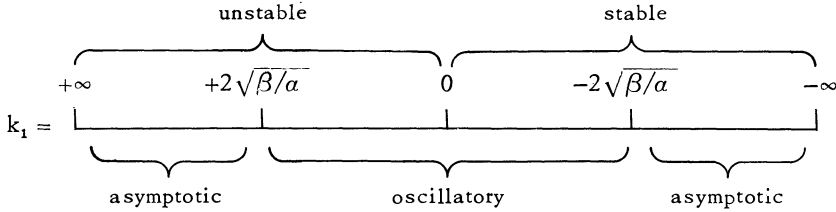
Now from (6) when  $m$  is real (that is, when  $k_1^2 \geq 4\beta/\alpha$ )  $m^2$  and  $\alpha\beta$  are always positive, so that minus  $\alpha k_1 m$  must be negative in equation (6). But minus  $\alpha$  is always negative; therefore  $k_1 m$  must be positive; therefore  $k_1$  and  $m$  must have the same sign. From (3a) and (4a) we see that if  $m$  is positive, the interaction is unstable (limit of both  $y$  and  $x = \infty$  as  $t \rightarrow \infty$ ); if it is negative, the interaction is stable (limit of both  $x$  and  $y = 0$  as  $t \rightarrow \infty$ ). But  $k_1$  must be negative for  $m$  to be able to be negative; therefore  $k_1$  must be negative for stability to exist close to community equilibrium when  $m$  is real. No oscillatory properties can be attributed to  $m$  when it is real.

When  $m$  is complex (that is,  $k_1^2 < 4\beta/\alpha$ ), however, we can express  $x$  this way (from 3a):

$$(8) \quad x \propto e^{mt} = e^{(a+bi)t} = e^{at}(\cos bt + i \sin bt).$$

Note that the real part of  $m$  is the only part of  $m$  qualifying stability; the sin and cos functions contribute the oscillations. The oscillations decay if and only if the real part of  $m$  is negative. From (7) we note that the real part is just  $\alpha k_1/2$  since we are dealing with the case where  $m$  is complex. Thus, for stability  $\alpha$  and  $k_1$  must differ in sign. But  $\alpha$  is always positive; therefore the interaction is stable if and only if  $k_1$  is negative. This is the

same conclusion we reach for the real case, and we have constructed the following chart.



From (8) we note that  $x$  completes one oscillation when  $bt$  goes from zero to  $2\pi$ , that is, when  $t$  goes from zero to  $2\pi/b$ . Thus  $x$  has period (from 7):

$$(9) \quad T = 2\pi/b = 4\pi/\sqrt{4a\beta - a^2k_1^2}.$$

Now let us combine equations (1) and (2a) and search for an  $m$  in the same manner.

$$(10) \quad \frac{dx}{dt} = mAe^{mt} = mx = \alpha(k_1x - y), \quad \text{or} \quad (ak_1 - m)x = \alpha y.$$

$$(11) \quad \frac{dy}{dt} = mBe^{mt} = my = \beta(x - y/k_2).$$

Solving (11) for  $x$  we obtain:

$$(12) \quad x = \frac{y(\beta/k_2 + m)}{\beta}, \text{ which upon substitution into (10) gives us:}$$

$$(13) \quad [m^2 + (\beta/k_2 - ak_1)m + \alpha\beta(1 - k_1/k_2)] = 0.$$

The two roots may be examined qualitatively by manipulating signs. Note that  $m^2$  is always positive (for real  $m$ ) as are  $\alpha$ ,  $\beta$  and  $k_2$ . As before,  $m$  must be negative for the system to be stable.

Case 1: If  $k_1$  is negative, then  $(1 - \frac{k_1}{k_2})\alpha\beta$  and  $(\frac{\beta}{k_2} - ak_1)$  are positive, therefore  $m$  must be negative and the system is stable.

Case 2:  $k_1$  is positive and  $k_1 \leq k_2$  so that  $\alpha\beta(1 - k_1/k_2) \geq 0$ :

(a) If  $k_1 \leq \frac{\beta}{ak_2}$ , so that  $(\frac{\beta}{k_2} - ak_1) \geq 0$ , then  $m$  must be negative and the system is stable.

(b) If  $k_1 > \beta/ak_2$ , so that  $(\beta/k_2 - ak_1) < 0$ , then  $m$  must be positive and the system is unstable. All of the above conditions also hold for  $m$  when it is complex. This may be proved by an analysis like that case for (1) + (2b).

Case 3: If  $k_1 > k_2$ , an isocline diagram reveals the instability most simply, but in this case another community equilibrium point is present which may have stable properties. In any event, this seems to be an unrealistic

instance, for it implies that the predator is able to increase at the extremely low densities of prey where the prey themselves can no longer increase.

A summary of these stability properties is contained in figure 6. In general, decreasing the slope  $k_2$  from infinity to some number, increases the number of possible stable systems.

Another way of modifying the continuous model is to insert vectors of discrete length at each point rather than view them as continuously changing. We are currently analyzing such a situation.

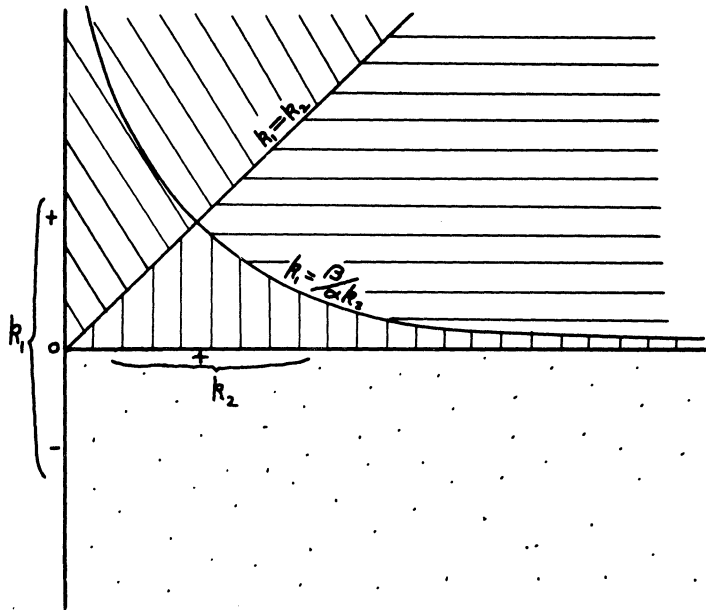


FIGURE 6. Comparative values of  $k_1$  and  $k_2$ , and resultant stability close to interaction equilibrium (see text for complete analysis) for situation (1) and (2a). Dotted area is Case 1; vertical cross-hatching is Case 2a; horizontal cross-hatching is Case 2b; diagonal cross-hatching is Case 3.

Summarizing the stability properties around the community equilibrium point, we first note that the prey slope must almost always be negative for stability and the greater the negativity of  $k_1$ , the more stable the interaction. No relatively large positive  $k_1$  value will support stability. In the second case, the mere presence of a predator isocline slope,  $k_2$ , increased the possible values of  $k_1$  for which the relationship would be stable.

#### SOME RESULTS OF EVOLUTION ON THE STABILITY OF THE INTERACTION

Keeping these stability properties in mind, let us examine the evolutionary properties of our graph. A predator who can kill enough prey at a given prey density to maintain himself and enough offspring to replace himself will be more fit than a predator who cannot kill at a great enough rate to accomplish this (when given the same prey density). Natural selection

will thus increase the predator's ability to kill prey; in other words, the predators are able to just maintain themselves at a constantly decreasing density of prey. The predator isocline moves left. This action always decreases stability.

However, the prey at this lower equilibrium density have suffered a decrease in the absolute number of offspring they can bring into the world and an increase in the rate at which they are being killed. They therefore will not usually be able to maintain themselves at the old predator density, let alone any higher one. This type of selection on the predator, therefore, also depresses the prey isocline. Due to this fact, increasing predator efficiency by increasing the predator's ability to kill may well result in decreasing the community equilibrium density of predators. Also,  $k_1$  at equilibrium is certainly less steep. If the interaction was previously locally stable, stability is then decreased. If it was unstable before ( $k_1 > 0$ ), it may become less unstable, but does not change to stability.

The opposite of this selective force is the selection of the prey which are best able to avoid being eaten. This tendency toward decreasing the rate of kill (or better, the rate of being killed) moves the predator isocline to the right and raises the prey isocline. It is thus a probable factor in increasing stability.

Efficiency of the predator may also be increased by selecting those better able to utilize the same amount of kill. This would still move the predator isocline left, but because the predation rates remain the same at each prey density, it would have no effect on the prey's isocline. In this way, the predators could increase their density at community equilibrium, but they are again decreasing the stability of the interaction.

Another method of increasing the interaction equilibrium value of the predator is to increase his absolute food supply. A priori, there seems to be only one way in which this can be done, and that is to increase or at least maximize the percentage of prey food turned into more prey. Graphically (if we plot prey biomass instead of number), this raises the prey isocline, steepening its slope and thus probably increasing stability. Although this seems far-fetched, it has actually been observed in the field by Connell (1961). The gastropod, *Thais lapillus*, which is able to open only a limited number of its prey, the barnacle, *Balanus balanoides*, per unit time, has naturally evolved in the direction of opening only the largest barnacles (these provide the most food per unit time). Coincidentally, these barnacles are the slowest growing of all (the growth rate of a barnacle decreases with age). This means that *Thais lapillus* was simultaneously evacuating the greatest barnacle space, and leaving the fastest growing barnacles. The predator was maximizing the amount of barnacle food converted to barnacle per unit time, though it accomplished this coincidentally with, and not directly by, natural selection. Of course, the predator, by opening the largest prey, was also increasing its efficiency, thus moving its isocline left, decreasing stability, and balancing (to an unknown extent) the effect of raising its prey isocline.

Such coincidences are probably rather widespread phenomena. Vertebrate predators may be seen to attack, preferentially, the dead and the dying (Allen, 1962), that is, those prey with the least reproductive value. This is coincidental with the fact that these are the very same prey which are least able to resist. Predators who can detect and preferentially attack such prey will be most efficient (MacArthur, 1960). A predator with this ability will most likely have little effect on the reproductive potential of its prey when he himself is scarce, that is, the lower right part of the prey's isocline will approach (or even reach) verticality. Thus this is also a force causing the approach to a maximum oscillation.

Natural selection, with regard to the continuous model, when acting on the predator, usually tends to increase its efficiency and destabilize the interaction; selection on the prey tends to increase stability. There is as yet no known force within the predator population acting specifically to conceive of and enforce the best strategies for maintaining the predator population at a maximum density. Efficiency selection on the predators appears to be blind with respect to the group, and changes the interaction in favor of the individual predator, even when doing so involves decrease of the total number of predators in the population.

#### SUMMARY

The general nature of the predator-prey interaction has been depicted as a graph of predator versus prey densities from which conditions for stability of the interaction are predicted. An example of a three-species interaction is also presented. Variations of the graph are introduced, and it is shown that an otherwise unstable interaction may be stabilized by the presence of either an inviolable prey hiding place, or extremely low predation pressure at moderate predator and high prey densities, or another predator-limiting resource. Stability is always conferred when the predator is severely limited at its equilibrium density by one of its resources other than its supply of prey. Predators should tend to be limited at their equilibrium densities by more than one of their resources. When either of the two foregoing situations pertains, regular predator-prey oscillations should not be observable.

The stability of the interaction close to equilibrium was found to depend exclusively, in the mathematically-continuous model, upon the slopes of two lines in the graph at equilibrium. Stability can be asymptotic rather than oscillatory in type. An equation for the period of oscillatory interactions is also advanced. The effects of Natural Selection on the isoclines, and thus the stability, is not clear-cut. Selection of the prey tends to stabilize the interaction; the opposite is true for selection on the predator.

#### ACKNOWLEDGMENTS

One author was supported by a graduate fellowship from the National Science Foundation, and the other by grant G-11575 from the same Foundation.

The authors both wish to thank Mrs. Rosenzweig, whose help and patience in typing and retyping their manuscript were infinite.

## LITERATURE CITED

- Allen, Durward L., 1962, Our wildlife legacy. Rev. ed. Funk and Wagnalls, New York. 422 pp.
- Andrewartha, H. G., and T. O. Browning, 1961, An analysis of the idea of "resources" in animal ecology. *J. Theoret. Biol.*, 1: 83-97.
- Christian, J. J., 1961, Phenomena associated with population density. *Proc. Nat. Acad. Sci. U. S.*, 47: 428.
- Connell, J. H., 1961, Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle, *Balanus balanoides*. *Ecol. Monographs*, 31: 61-104.
- Crowell, K., 1961, Effects of reduced competition in birds. *Proc. Nat. Acad. Sci. U. S.*, 47(2): 240-3.
- Holling, C. S., 1959, The components of predation as revealed by a study of small-mammal predation of the European sawfly. *Can. Entomol.*, 91(5): 293-320.
- Huffaker, C. B., 1958, Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia*, 27: 343-383.
- Lotka, A. J., 1932, The growth of mixed populations; two species competing for a common food supply. *J. Wash. Acad. Sci.*, 22: 461-469.
- MacArthur, R. H., 1960, On the relation between reproductive value and optimal predation. *Proc. Nat. Acad. Sci. U. S.*, 46(1): 143-145.
- Slobodkin, L. B., 1961, Growth and regulation of animal populations. Holt, Rinehart, and Winston, New York. 184 pp.
- Utida, S., 1957, Population fluctuation, an experimental and theoretical approach. *Cold Spring Harbor Symp. Quant. Biol.*, 22: 139-151.