A SIMPLE MODEL OF MUTUALISM

ANTONY M. DEAN*

Department of Biological Sciences, Illinois State University, Normal, Illinois 61761

By definition (Odum 1971), mutualism is the interaction of two species of organisms that benefits both. Obligate mutualists may survive only by association; facultative mutualists, while benefiting from the presence of each other, may also survive in the absence of each other. Mutualisms are found in many diverse communities; such interactions are well documented in the field. Examples include the algal-fungal associations of lichens (Ahmadjian 1967; Hale 1974); plant-pollinator interactions (Janzen 1971); seed dispersal systems that rely on animal vectors (McKey 1975); the legume-nitrogen-fixing bacteria interactions (Burns and Hardy 1975); and damselfish-sea anemone interactions (Roughgarden 1975).

Despite the fact that mutualisms are not uncommon in nature, attempts to model such interactions mathematically are somewhat scant in the literature. Models attempting to describe mutualist interactions between two species have been based on modifications of the well-known Lotka-Volterra competition equations (e.g., see May 1976). Only by limiting the amount of mutualist interaction or by introducing nonlinearities without biological meaning may the models predict that a stable equilibrium will exist. Otherwise, the models suggest that the interacting populations will grow to unlimited proportions; a notion that is biologically absurd. Obviously for such populations there exist saturation levels determined by factors such as limited space or food resources. Yet such factors are left external to these models (Vandermeer and Boucher 1978) so that the models cannot be used to determine the effects of these factors on the mutualists.

Incorporation of a third species, as a predator or as a competitor, to stabilize the mutualism has been attempted (Heithaus et al. 1980). Such a model allows a stable equilibrium to be reached, even when the two mutualist species involved would undergo unlimited growth in the absence of the third. While I do not wish to argue that many mutualistic interactions may be stabilized principally by such interactions as predation and competition, surely in the absence of the latter, mutualisms should reach some sort of equilibrium because of other limiting factors such as food availability. As such, the model may be unrealistic for a large number of

* Present address: Department of Genetics, Washington University School of Medicine, St. Louis, Missouri 63110.
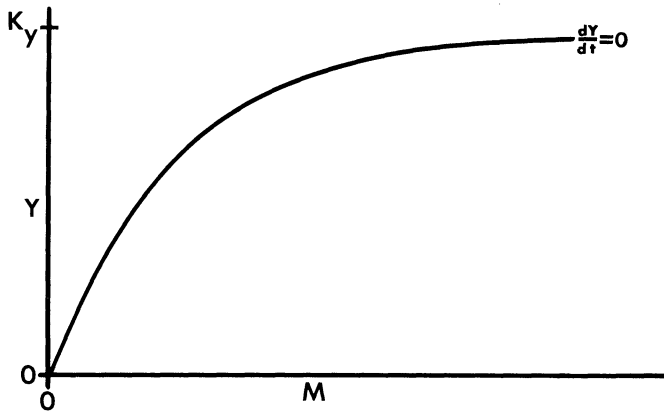
FIG. 1.—The relationship between the carrying capacity, k_y, as defined by the isocline $dY/dt = 0$, for a species utilizing an environmental resource, M. The curve asymptotes as the level of the resource increases and so no longer becomes limiting; other environmental factors now limit the carrying capacity to K_y.

mutualisms for which the effects of predation and/or competition by a third species are minor compared with other factors.

The model proposed here uses density dependence as the principal mode by which two mutualists reach a stable equilibrium; any other interactions merely modify it.

THE BASIC MODEL

Suppose that a species, Y, is allowed to grow in a stable and unchanging environment until its carrying capacity, k_y, is reached. Further, suppose that an environmental variable, M (such as the constantly replenishable food resource of a chemostat), limits k_y and may be experimentally controlled. Then for any given value of M, the species will grow to a particular k_y. However, as M increases other environmental factors will begin to limit the value of k_y, such that even with unlimited M, k_y will reach a maximum, K_y. The simplest model describing the relationship between k_y and M is as follows:

$$\frac{dk_y}{dM} = \frac{a(K_y - k_y)}{K_y}. \tag{1}$$

The above equation assumes that the constant, a, is reduced by a linear function of k_y. Upon integration the above equation yields:

$$k_y = K_y\{1 - \text{EXP}[-(aM + C_y)/K_y]\} \tag{2}$$

in which C_y is the integration constant. The above relationship is illustrated in figure 1. Since, by definition, any value of Y that falls on this curve is at a point

when the growth of the population is zero (so $Y = k_y$), equation (2) describes the isocline where $dY/dt = 0$.

In the case of mutualism, let M represent the density of the mutualist species X. Because it is permanent, X is effectively a replenishable resource, which is certainly true in principle of the nectar resources of many pollinators. Then equation (2) may be rewritten as follows:

$$k_y = K_y\{1 - \text{EXP}[-(aX + C_y)/K_y]\}. \tag{3}$$

However, in the case of mutualism, the carrying capacity of species X, k_x, will be dependent on the value of Y. Therefore, the relationship between k_x and Y may be described as follows:

$$k_x = K_x\{1 - \text{EXP}[-(bY + C_x)/K_x]\} \tag{4}$$

in which K_x is the maximum value of k_x, C_x is the integration constant, and b is a constant and is equivalent to a in equation (1).

Graphically, the condition that allows mutualism to occur is that the isocline $Y = k_y$ ($dY/dt = 0$) runs above the isocline $X = k_x$ ($dX/dt = 0$) for some interval. Algebraically this condition will be satisfied if any value of X or Y can be found to satisfy one or other of the following equations:

$$K_y\{1 - \text{EXP}[-(aX + C_y)/K_y]\} > -\{C_x + K_x[\ln(K_x - X) - \ln K_x]\}/b \tag{5}$$

or

$$K_x\{1 - \text{EXP}[-(bY + C_x)/K_x]\} > -\{C_y + K_y[\ln(K_y - Y) - \ln K_y]\}/a. \tag{6}$$

The above may be explained in biological terms as follows. All that is required is that the number of one mutualist maintained by a certain number of the other mutualist be greater than the number of the former needed to maintain that certain number of the latter. If true, then both populations will grow until the density effects limit the growth of the carrying capacities of X and Y, so that the isoclines 3 and 4 will inevitably intersect at a point of stable equilibrium (fig. 2a). Figure 2b shows the unstable equilibrium formed when the two isoclines touch. If an environmental perturbation causes one or both of the species to be reduced in number, such that the point falls into the hatched region, then this will result in the extinction of both species. In figure 2c, the isoclines do not touch or intersect and, therefore, no mutualism may occur.

The rates of growth of the two mutualist species may be described by modified logistic growth equations as follows:

$$\frac{dY}{dt} = \frac{r_y(k_y - Y)Y}{k_y} \tag{7}$$

$$\frac{dX}{dt} = \frac{r_x(k_x - X)X}{k_x} \tag{8}$$

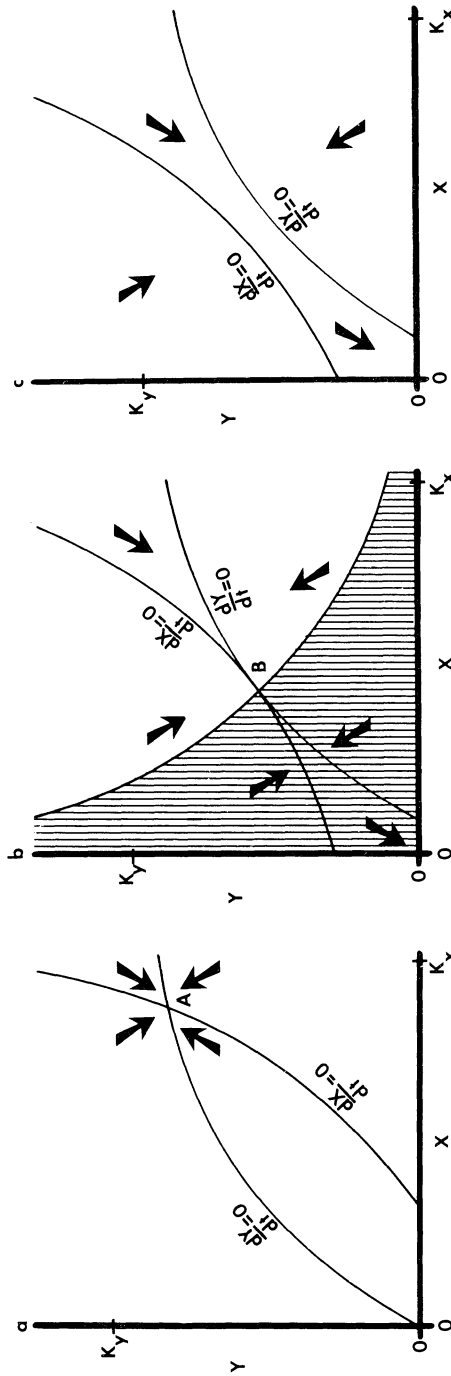in which r_y and r_x are the intrinsic rates of increase of species Y and X, respec-

FIG. 2.—Isoclines for two mutualistic interacting populations. a, The isoclines intersect at a point A which is stable as indicated by the trajectories. b, The isoclines touch, resulting in an unstable point of equilibrium B. Trajectories originating in the unhatched region are attracted to B; those in the hatched region to the origin. c, The isoclines do not meet and so all trajectories approach the origin. Thus, in b and c no mutualism may exist.

tively. Note that k_y and k_x are not constants (as they are in the logistic equation), and are determined by equations (3) and (4).

DISCUSSION

Types of Mutualism

The signs of the integral constants determine the type of mutualism that may occur. The three basic types of mutualism, facultative, obligate, and obligate with thresholds, are illustrated in figure 3. If both C_x and C_y are positive, then facultative mutualism will inevitably occur: Each species will be able to survive in the absence of the other. The integral constants, therefore, represent other resources utilized by the mutualists. Note, however, that the model proposed assumes that there are no complex interactions between the resources and the mutualists (such as majoring on the other mutualist in preference to the resources represented by the integral constants). If $C_x = C_y = 0$, then obligate mutualism will occur if $ab > 1$. This is obvious, since if, at the origin, the isoclines are parallel ($ab = 1$) or if $ab < 1$ then the isocline $Y = k_y$ cannot run above the isocline $X = k_x$. If both C_x and C_y are negative, then the model predicts that the only type of mutualism possible is obligate, and that thresholds exist before the species may benefit from each other's presence. If the threshold levels are not met, then the extinction of both species will ensue.

Of the many other possibilities for mutualist interactions predicted by this model, two are illustrated in figure 4. In both 4a and 4b, C_y is positive and C_x negative. However the relative magnitudes of the integral constants yield different results. In 4a species Y makes facultative use of species X and species X obligate use of species Y. So long as Y exceeds the threshold level, mutualism will occur. Since at $X = 0$ Y exceeds this level, if X is at all present, mutualism will occur. However, in 4b the threshold level is greater than Y at $X = 0$, thus a threshold and unstable point of equilibrium exist. If a point lies in the unhatched region, then mutualism will occur. However, if the point lies in the hatched region, then mutualism will not occur since species X will become extinct, even though species Y will persist alone.

The Stability of Mutualisms

In figures 2b, 3c, and 4b a boundary exists between the two domains of attraction (the hatched and unhatched regions). Analysis of these domains has not been carried out in any of the three cases. Obviously, if either of the two species is rare and the other extremely common the stable point at the origin will be attractive. Thus the domain of attraction of the origin (the hatched region) must be asymptotic to the axes and also pass through the unstable point of equilibrium. The phase space is evidently split by a ridge separating the domains of attraction of the two stable points, and may be shaped rather like those in the figures. The boundary (ridge) was calculated in one special case. Points on the boundary are very likely to converge to the unstable point of equilibrium along this curve.
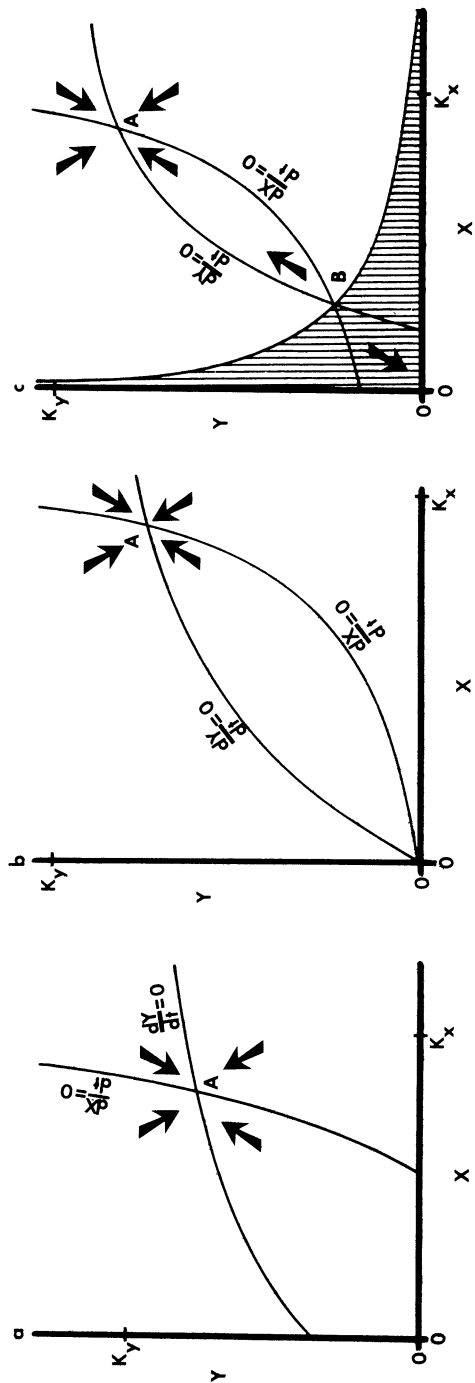
FIG. 3.—The effect of the integral constants upon the type of mutualism exhibited. *a*, Both integral constants are greater than zero, so both interacting species are facultative mutualists. *b*, Both integral constants are zero, so both species are obligate mutualists. *c*, Both integral constants are less than zero, so both species are obligate mutualists and thresholds exist.
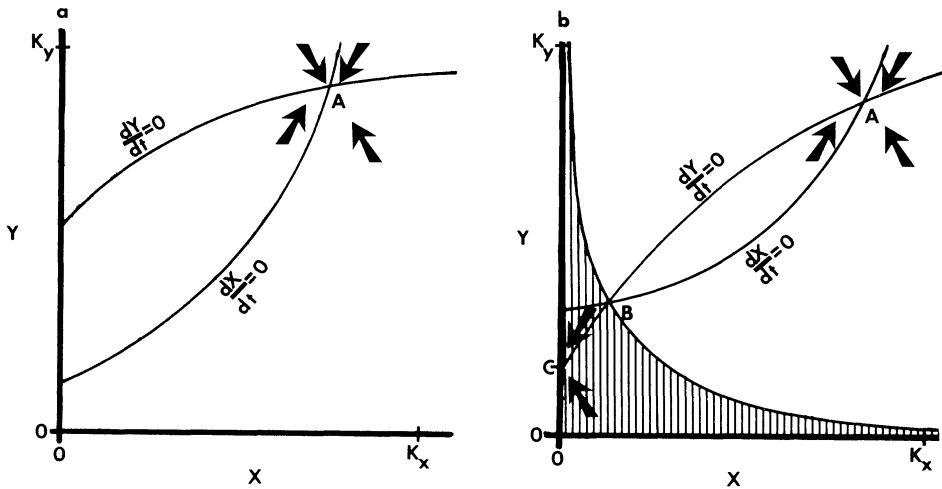
Fig. 4.—*a*, The integral constants assume different signs. $C_y > 0$ and $C_x < 0$. Thus Y is a facultative mutualist and X an obligate one. *b*, The integral constants assume the same signs as in *a*, but their magnitudes are such that an unstable point of equilibrium exists.

However, the boundary is of little biological significance because real populations fluctuate stochastically in size and so will enter one region or the other. The asymptotes are also not of any real interest since stochastic fluctuations will easily move populations from one region to the other.

The boundary will be determined by a number of factors. Obviously, the unstable equilibrium is determined by the signs and magnitudes of the integral constants C_x and C_y as well as constants a, b, K_x, and K_y. If time lags are introduced such that one species only reacts to the other after some time delay, the intrinsic growth rates may have pronounced effects. For example, if a point exists in the hatched region of the simple model so far proposed, extinction of one or both mutualists should follow. However, if time lags are included in the model, then growth of one or both mutualists might still take place. As a result, the unhatched region might be attained, resulting in the perpetuation of the mutualism. As such, the mutualism will be far less sensitive to environmental perturbations than the simple model would predict; that is, the hatched region will have been reduced.

As May (1976) points out, the existence of such a boundary may at least partly explain the observation that obligate mutualisms are far more prevalent in tropical ecosystems than in more seasonal (and by inference, less stable and predictable) environments. The type of mutualism to be favored in the latter case therefore would appear to be a facultative association between two or more mutualists. Indeed, because facultative mutualisms allow the species to exist independently of one another, this type of mutualism was probably the first to evolve. That it is so prevalent today, especially in the more temperate zones, is testimony to the success of such an evolutionary strategy.

The modified Lotka-Volterra competition equations and those discussed by Meyer et al. (1975) suggest that mutualisms must be stabilized by factors external to these simplest of models. Competition or predation by a third species (Heithaus et al. 1980), the introduction of rate-limiting resources, competition for a rate-limiting resource, and inhibitory resources (Meyer et al. 1975) may each stabilize the models under certain conditions. Here, stability arises from the fact that the carrying capacities of the mutualist populations are dependent upon each other's abundance, showing diminishing returns as they increase. The populations are therefore self-limiting because the members of each population compete for limited resources.

SUMMARY

A population of mutualists must eventually reach a maximum carrying capacity because of intraspecific competition for limited resources, even if another population of mutualists is present in excess. The model presented reflects this, so allowing a stable equilibrium to be reached. Either facultative or obligate use of one mutualist by another is seen to be independent of whether the former makes facultative or obligate use of the latter. Given that a mutualism may occur, facultative use by both populations will inevitably lead to a stable equilibrium no matter the initial densities of the populations; but if one population makes obligate use of the other, then thresholds may occur such that the mutualism will be sensitive to environmental perturbations.

LITERATURE CITED

Ahmadjian, V. 1967. The lichen symbiosis. Blaisdell, Toronto.

Burns, R. C., and R. W. F. Hardy. 1975. Nitrogen fixation in bacteria and higher plants. Springer-Verlag, New York.

Hale, M. E., Jr. 1974. The biology of lichens. 2d ed. Arnold, London.

Heithaus, E. R., D. C. Culver, and A. J. Beattie. 1980. Models of some ant-plant mutualisms. Am. Nat. 116:347–361.

Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. Science 171:203–205.

McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pages 159–191 in L. E. Gilbert and P. E. Raven, eds. Coevolution of animals and plants. University of Texas Press, Austin.

May, R. M. 1976. Models for two interacting populations. Pages 49–71 *in* R. M. May, ed. Theoretical ecology: principles and applications. Saunders, Philadelphia.

Meyer, J. S., H. M. Tsuchiya, and A. G. Fredrickson. 1975. Dynamics of mixed populations having complementary metabolism. Biotech. Bioeng. 17:1065–1081.

Odum, E. P. 1971. Fundamentals of ecology. 3d ed. Saunders, Philadelphia.

Roughgarden, J. 1975. Evolution of marine symbiosis—a simple cost-benefit model. Ecology 56:1201–1208.

Vandermeer, J. H., and D. H. Boucher. 1978. Varieties of mutualistic interaction in population models. J. Theor. Biol. 74:549–558.