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LYCAENID BUTTERFLIES AND ANTS: TWO-SPECIES STABLE
EQUILIBRIA IN MUTUALISTIC, COMMENSAL, AND
PARASITIC INTERACTIONS

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The larvae of many species in the butterfly family Lycaenidae associate with ants (for review, see Hinton 1951; Atsatt 1981; Cottrell 1983). Although few studies have attempted to assess the actual costs and benefits of the association for both partners (e.g., Ross 1966; Pierce and Mead 1981; Pierce 1983; Pierce and Eastal 1986), lycaenid butterflies and ants appear to exhibit all three kinds of interaction: mutualism, commensalism, and parasitism. Consideration of the natural history of lycaenid-ant associations has led us to develop a model in which the presence of lycaenids affects the equilibrium density of their attendant ants, and the presence of ants influences both the growth rate and equilibrium density of the butterflies. This single model can describe facultative as well as obligate interactions. Moreover, even when the association is mutualistic, the model possesses globally stable equilibria.

The main emphasis of our model is the observation that one of the species in the association exhibits two dramatically distinct life stages, interacting with its partner during only one of those stages. Thus, in the particular example discussed here, the butterflies are holometabolous, and only the immature stages interact with ants. This is just one example of a general characteristic of many symbioses, including plant-pollinator relationships, certain homopteran-ant associations, and a great variety of interactions in marine systems. In lycaenid-ant associations, the presence of ants influences the fraction of pupae that eclose into adults. The subsequent dynamics of the butterfly population is not affected by ants. In particular, the number of butterflies that survive to lay eggs is not altered by the ant population. However, the effect of lycaenids on attendant ants is characterized by the more traditional notion that food supplies affect the number of ant colonies capable of existing in a given environment. In other words, the equilib-

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rium density of the ants is raised in mutualistic associations and lowered in parasitic ones.

A possible example of a mutualistic interaction between lycaenids and ants is that of the Australian lycaenid *Jalmenus evagoras* and its attendant ants, *Iridomyrmex* sp. 25 (Australian National Insect Collection, *anceps* group; see Pierce 1983). The immature stages of *J. evagoras* secrete substantial food rewards in the form of sugars and amino acids that the ants harvest. For example, 67 juveniles of *J. evagoras* living on a single food plant secreted approximately 400 mg of dry biomass for their attendant ants over a 24-h period (Pierce 1983). In return for this food, ants protect larvae and pupae against parasitoids and predators. Field experiments with this species showed that parasitism of and predation on the immature stages are so intense that without attendant ants, populations of *J. evagoras* would not survive (Pierce 1983). Ants are sufficiently important in the life history of *J. evagoras* that females use them as cues in selecting sites for oviposition (Pierce and Elgar 1985).

A likely commensal relationship between lycaenids and ants is that of *Deloneura ochrascens* (Jackson 1937). The larvae of this butterfly are found with ants of the species *Crematogaster castenea* among lichens on tree bark (*Acacia stenocarpus*). The larvae feed on the lichen and do not interact with the ants. Nevertheless, larvae often nestle in the entrances of the ant galleries, probably gaining protection from their proximity to the ants. Other African species such as *Iridana incredibilis* and *I. perdita marina* have similar life histories (Jackson 1937).

Finally, a clear case of lycaenid-ant parasitism is that of the large blue, *Maculinea arion*, and its attendant ant, *Myrmica sabuleti* (Frohawk 1903; Chapman 1916; Thomas 1980; Cottrell 1983). Larvae of *M. arion* secrete substances that mimic ant-brood recognition signals. A developing larva feeds on flowers of thyme, *Thymus drucei*, until after the third molt, whereupon it drops to the ground and awaits discovery by a worker of *M. sabuleti*. As soon as a worker finds the larva, she picks it up, carries it into the nest, and places it with the brood. Undetected by the ants, the larva becomes predaceous and feasts upon the brood. It grows to a large size, overwinters, and pupates in the ant nest.

ASSUMPTIONS OF THE MODEL

Our model stresses the following features of the natural history of lycaenid-ant interactions.

1. Mutualistic lycaenids supply nutrients for the ants, thereby increasing the number of ant colonies that can survive in a given environment. Nutrition is important to both the survival of queens and the production of new queens (e.g., Wilson 1971; Brian 1983). Hence, the presence of mutualistic lycaenids could raise the equilibrium density of the ant population. Commensal interactions have no effect on the equilibrium density of the ants, but parasitic interactions decrease the equilibrium density (fig. 1).

2. Our previous remarks about holometaboly suggest that there are really three interacting populations in our model: immature lycaenids, adult lycaenids, and

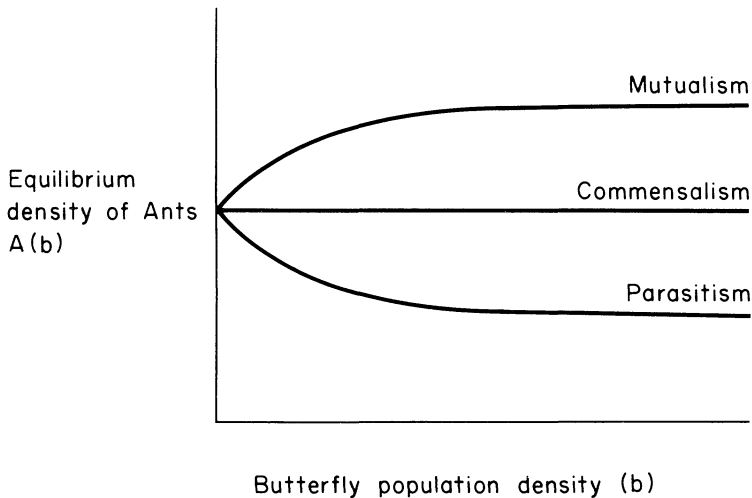


FIG. 1.—Three cases of the equilibrium density of the ants, $A(b)$, as a function of the butterfly population density, b : if the interaction is mutualistic, $A(b)$ increases with b ; if the interaction is commensal, $A(b)$ is constant; if the interaction is parasitic, $A(b)$ decreases as b increases. In all cases, the effect “saturates” and $A(b)$ approaches a constant as b approaches infinity.

ants. For simplicity we have lumped the first two into a single variable, the density of adult lycaenids, and assumed that this variable also reflects the population density of immature stages: the more butterflies present, the more larvae there are to feed the ants. It is possible to construct a three-variable model with one variable for each stage, but the additional complexity of the mathematics obscures the presentation. If our goal were detailed quantitative prediction rather than qualitative understanding, such a construction would be useful.

3. The primary effect of the ants on the butterflies is to protect the immature stages. This protection alters the growth rate of the butterfly population (fig. 2) by increasing the realized fecundity of individual butterflies: in the presence of ants, a larger proportion of the eggs laid by any one butterfly will survive and eventually emerge as adults. Again, the natural history feature emphasized here is that the ecological niche occupied by juveniles is different from that occupied by adults. In this case, ants interact with the larvae and pupae of lycaenids, but not with the adults. In our model, the “birth” rate of butterflies is equivalent to the number of pupae that eclose. Because ants protect the larvae and pupae, mutualistic interactions with ants increase the survival of immature stages, thereby increasing the eclosion rate of the butterflies. The presence of ants does not affect the survival of butterflies, however, since ants do not interact with the adults. In the parasitic case described above (*Maculinea arion*), ants provide larvae with food and protection, and we can consider the ant nest itself analogous to a womb for the developing butterflies. The effect of the ants that nurture the larvae within the nest is to raise the eclosion rate of the butterflies.

4. Because lycaenid butterflies are holometabolous, a large fraction of each

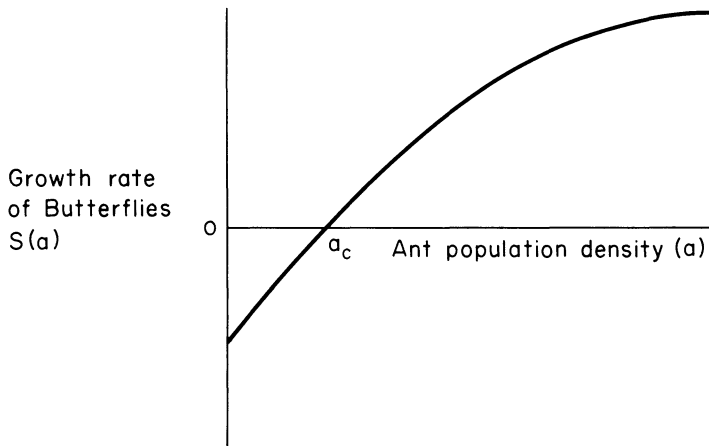


FIG. 2.—The intrinsic growth rate of the butterflies, $S(a)$, as a function of the ant population density, a . At low ant densities $S(a)$ is negative because of intense parasitism and predation. There is a critical size of the ant population, a_c , at which the growth rate of the butterfly population becomes positive. At large values of a , the effect saturates (all larvae survive) and $S(a)$ approaches a constant.

individual's life is spent as an egg, larva, and pupa. The majority of the foraging responsible for growth and eventual gamete production occurs in the larval stage, and this life history stage is probably most vulnerable to predation and parasitism. Hence, the equilibrium density of the butterflies is strongly influenced by the number of juveniles that survive to eclosion, and survival rate depends on the ant population size. In addition, the equilibrium density of the butterflies will be regulated by density-dependent controls, such as predation and shortages of food supplies, that are independent of the number of ants. Both of these ant-dependent and ant-independent effects have been incorporated into our model.

THE MODEL

The model we propose is an extension of the classical Lotka-Volterra equation for population growth, and is expressed as

$$da/dt = ra - r[a^2/A(b)] \quad (1)$$

$$db/dt = S(a)b - S_0(b^2/B), \quad (2)$$

where a is the population density of the ants (in terms of numbers of ant colonies); b , the population density of the butterflies; r , the intrinsic growth rate of the ants; $A(b)$, the equilibrium density of the ants, which depends on the butterfly population density (fig. 1); $S(a)$, the intrinsic growth rate of the butterflies, which depends on the ant population density (fig. 2); S_0/B , a constant of the environment regulating the population density of the butterflies; and $BS(a)/S_0$, the equilibrium density of the butterflies, which depends on the ant population density.

Note that $S(a)$ is negative if $a < a_c$; a_c is the critical ant population density

required to ensure that the growth rate of the butterfly population is positive. If there are not enough attendant ants, parasitism and predation on larvae are so intense that the butterfly population has a negative growth rate and becomes extinct. The model can also describe facultative mutualism by simply assuming that $S(a)$ is always positive and that there is no critical number of ants necessary for the butterflies to survive.

In constructing the model, we decided to use the form in equation (2) rather than a superficially similar form:

$$db/dt = S(a)b - S(a)b^2/B. \quad (3)$$

The difference between the two is most easily appreciated by considering the behavior of the butterfly population density when

$$b/B \gg 1 \quad (4)$$

(i.e., a butterfly epidemic). In this case, equation (2) reduces to $db/dt \equiv -S_0(b^2/B)$, and the decrease in density is independent of the ant population density. We introduce the symbols S_0/B separately rather than as a single constant so that the analogy with the standard Lotka-Volterra equation is more apparent. Dimensional analysis is also made easier: S_0 has the dimension 1/time and B has the dimension butterfly population size.

Alternatively, in the limit (4), equation (3) gives $db/dt \equiv -S(a)b^2/B$, and the rate of decrease of the butterfly population is influenced by the population density of the ants through $S(a)$. This latter possibility seems unrealistic in view of the natural history of the system: the ants increase the growth rate of the butterflies by ensuring that a larger fraction of the larvae survive and metamorphose into butterflies. Since the ants have no effect on the mortality of butterflies, they cannot influence the rate at which epidemic populations of butterflies decrease. Other processes signified by the constant S_0/B that are independent of the ant population density, such as predation or starvation, are the controls that determine the equilibrium density of the butterflies under these situations. Hence, the system described by equations (1) and (3) has several biologically unreasonable equilibria whose existence is due solely to ant-dependent behavior of the butterfly population when (4) is satisfied. The system of equations (1) and (2) is a more faithful translation of biological intuition into mathematics.

Several further refinements to our model might be considered. It is possible that butterflies also affect the growth rates of ants by increasing the numbers of reproductives produced by ant colonies (for discussion, see Wilson 1971; Brian 1983). This effect could be included by positing that r in equation (1) is a function of b . In addition, the larvae and butterflies could be treated as separate variables using a three-component model (see above). In the same vein, one could convincingly argue that for a species in which single generations are clearly separated by a seasonal cycle (as with *Glaucopsyche lygdamus* in Colorado; see Pierce and Eastal 1986), a difference equation might be a more appropriate model than equation (1). Even for species whose generations overlap (as with *Jalmenus evagoras* in Australia; see Pierce 1983), the time lag between egg deposition and the emergence of the reproductives might be important as a stabilizing mechanism, and it could be modeled using delay-differential equations.

Some of these embellishments, such as the possible effect of butterflies on ant growth rate, are easily included but lead only to quantitative changes: the structure of equilibrium solutions and the separatrices in the phase planes remain unaltered. Others, such as time lags, have complicated consequences that might alter the conclusions of the model. Although it would be straightforward to construct a model that includes all of the above, it would not be easy to solve it. The present model is intended to illustrate a process in isolation, rather than to predict the outcome of several interacting mechanisms. The process is the stabilization of obligate and facultative symbioses by the noninteraction of the partners when one is in the reproductive stage.

We now discuss the three varieties of lycaenid-ant interactions in turn. The three cases are distinguished by the behavior of $A(b)$ (as shown in fig. 1). Figure 3 shows the (a, b) phase plane in mutualism. The arrows indicate the direction in which the system tends to move if it is at a particular point in the (a, b) plane. Also shown are the curves on which da/dt or db/dt is zero. For instance, from equation (1), da/dt is zero if $a = 0$ or $a = A(b)$. Equilibrium solutions are points at which both da/dt and db/dt are zero. These are indicated by heavy dots and are also numbered.

As figure 3 illustrates, the behavior of the system is not entirely independent of the functions of figures 1 and 2. The most important question is whether the starting number of ants, $A(0)$, is larger than a_c . That is, is the carrying capacity of the ant population in the absence of butterfly larvae larger than the critical density required to ensure a positive growth rate for the butterflies? It seems most likely that, in general, the answer to this question is yes (and $A(0) > a_c$, as shown in fig. 3i), simply because it is the easiest situation in which to imagine the system evolving. Nevertheless, a condition such as that described by figure 3ii is conceivable, particularly in unstable or seasonal environments in which $A(0)$ might fall below a_c . Both cases are examined here. First, suppose $A(0)$ is greater than a_c (fig. 3i). There is one globally stable equilibrium solution that eventually traps the system (equilibrium point 1). Note how the equilibria with $b = 0$ (i.e., points 2 and 3) are unstable.

But suppose that $A(0)$ is less than a_c . As figures 3ii and 3iii indicate, there are two possibilities. In figure 3ii, the growth rate of the butterfly population rises sharply once a exceeds a_c . There are now four equilibria solutions, two of which are locally stable, as indicated by the arrows. In solution 1, b is nonzero and the ants have an elevated population density. In solution 3, the butterflies are extinct ($b = 0$) and the ant population density is $A(0)$. The system is eventually trapped by one of these two stable equilibrium solutions. There is a watershed or separatrix (shown by the dashed line passing through the unstable solution 2), which separates the domains of attraction of the two locally stable solutions. Initial conditions above the watershed would eventually collapse into the valley bottom at point 1, while those below the watershed would go to point 3.

In figure 3iii, $A(0)$ is again less than a_c , but the growth rate of the butterfly population rises slowly as a increases. There are two equilibria, and only point 1 is stable. The butterfly population must become extinct in this situation.

Now consider commensalism. Figure 1 illustrates that this case is a transition between mutualism and parasitism, and a real system may lean toward one or the

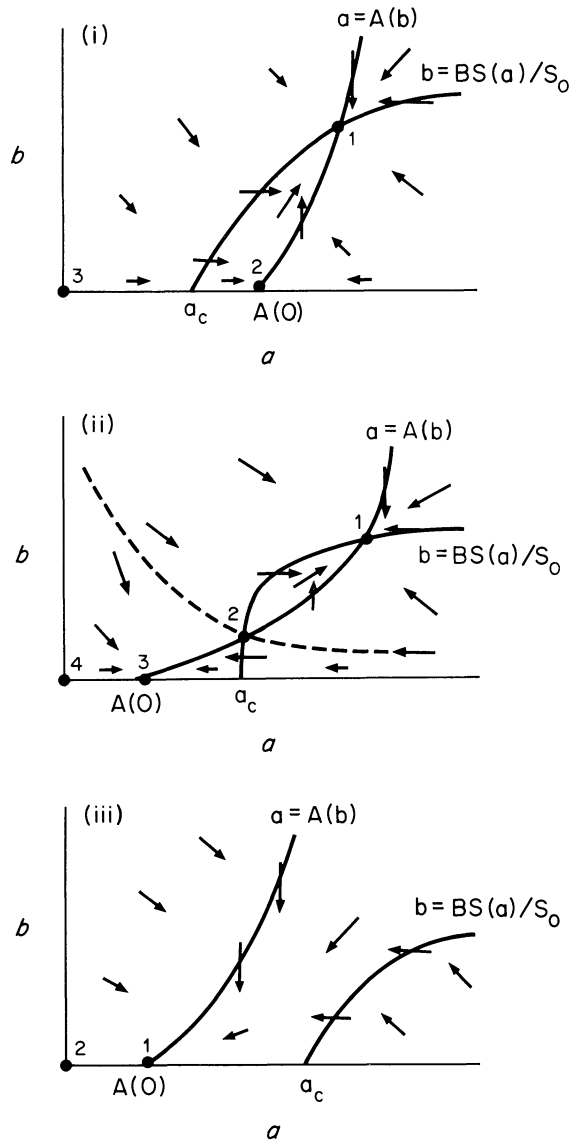


FIG. 3.—The (a, b) plane when the interaction is mutualistic. Arrows indicate the direction in which the system tends to move at a given point. (i), Equilibrium 1 is stable and 2 and 3 are unstable; (ii), equilibria 1 and 3 are stable; the dashed line delineates a separatrix dividing the domains of attraction of points 1 and 3; (iii), equilibrium 1 is stable. In all cases, if the system is displaced slightly from the stable equilibrium point, the displacement decreases exponentially without oscillations.

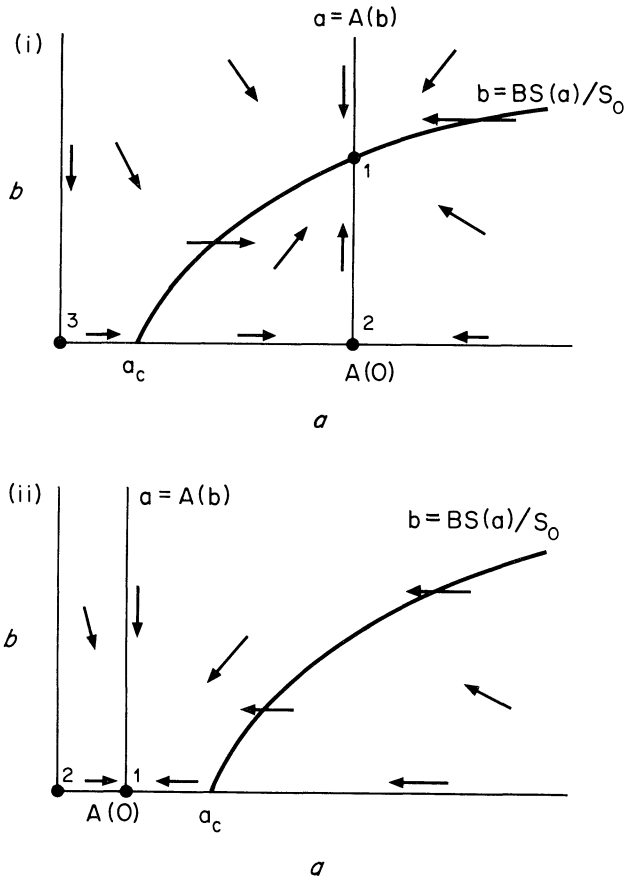


FIG. 4.—The (a, b) plane when the interaction is commensal. (i), Equilibrium 1 is stable and 2 and 3 are unstable; (ii), equilibrium 1 is stable, and the butterflies become extinct. Perturbations about the stable equilibria damp exponentially without oscillations.

other depending on the costs and benefits to each partner. Figure 4 shows the (a, b) plane. In this case $A(b)$ is a constant; that is, the changes in the ant population are independent of the butterfly population. Again the fate of the butterfly population hinges on whether $A(0)$ exceeds a_c . If the equilibrium density of the ants exceeds the critical density required to protect the butterfly population (fig. 4*i*), then the butterflies survive. In the other case (fig. 4*ii*), the butterflies become extinct.

Finally, suppose the interaction is parasitic. If $A(0)$ is greater than a_c , there is a stable equilibrium solution in which the butterflies survive (fig. 5*i*). Otherwise, the butterfly population becomes extinct (fig. 5*ii*). Figure 5*i* suggests that if the system is perturbed, the return to the equilibrium solution may take the form of damped oscillations. A straightforward linear stability analysis shows that this is possible if da/dt , evaluated at the equilibrium point, is sufficiently negative. This

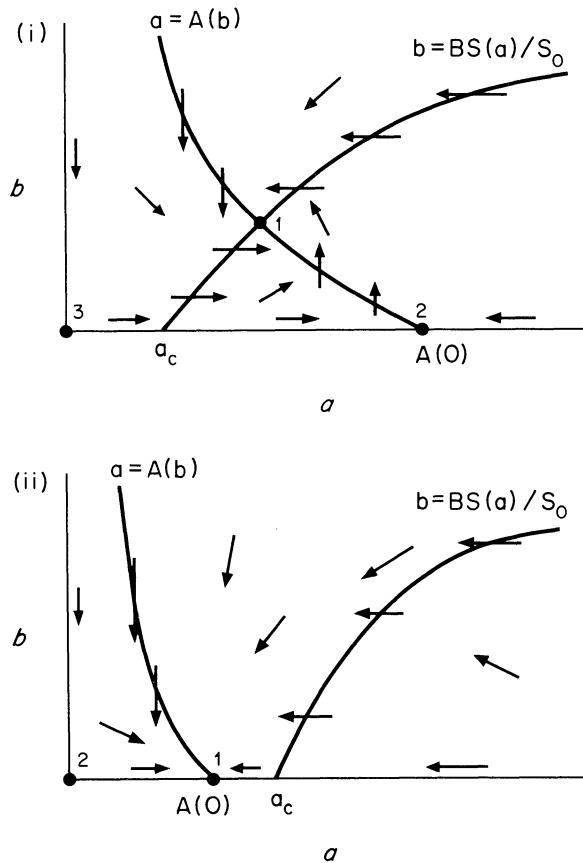


FIG. 5.—The (a, b) plane when the interaction is parasitic. (i), Equilibrium 1 is stable and 2 and 3 are unstable; (ii), equilibrium 1 is stable and the butterflies become extinct. If the system is displaced slightly from point 1, the return to equilibrium may take the form of damped oscillations.

same analysis indicates that small perturbations in all other cases decay without oscillation.

DISCUSSION

Previous models describing the population dynamics of mutualistic interactions have been based on the assumption that the presence of each species alters the equilibrium density of its partner (e.g., May 1973*a,b*; Levins 1974). In these models, depending on the values of the interaction coefficients, mutualism is unstable or destabilizing; in the welter of mutual enhancement, the population size of both species careens to infinity. Stable conditions are possible only with the addition of density-dependent interaction coefficients that ensure intraspecific regulation (e.g., Whittaker 1975; Christiansen and Fenchel 1977; Vandermeer and

Boucher 1978; Goh 1979; Dean 1983) or with external regulation from a third species such as a predator or competitor (Heithaus et al. 1980). May (1976), examining the stability of obligate mutualism at different population densities, found that at high population densities mutualisms could reach a stable equilibrium, whereas at low densities they were likely to become extinct. He reasoned from this that obligate mutualisms were more likely to evolve in the tropics, where environments might be more constant and both mutualists could maintain high population densities.

Addicott (1981) demonstrated in a numerical analysis that although certain mutualistic interactions may be unstable, others, perhaps the majority of cases, are relatively stable. He introduced a new class of models, of which ours is an example, in which the interaction between mutualists increases the equilibrium density of one species and the growth rate of another (a I-III interaction in Addicott's terminology). He argued that, in mutualism, "species derive benefit from each other in qualitatively different ways" (Addicott 1979, p. 43). This intuitive insight motivated his proposal of density-dependent growth rates. He then used computer simulations to analyze the return-time stability and persistence of six combinations of three basic two-species models (i.e., those of Gause and Witt 1935; Whittaker 1975; Addicott 1981). By comparing these models of mutualism with the appropriate models without mutualism, he determined that four of the six combinations showed higher return-time stability, and all models showed persistence stability. For example, if the interaction between two species increases the equilibrium density of one and the growth rate of another, then a perturbed system returns to equilibrium more rapidly when it is involved in a mutualistic interaction than when it is not.

Although our model falls into the same class of models introduced by Addicott, it differs from his analysis in several ways. First, we have based our model on the natural history of a particular system, identifying holometaboly as a biological mechanism underlying the "I-III" interactions described by Addicott. Second, our model can describe obligate mutualism as well as facultative mutualism, depending on the presence or absence of a_c in figure 2, and it encompasses parasitic and commensal relationships as well as mutualistic ones. This makes it particularly useful in describing lycaenid-ant associations, since all three types of interactions apparently occur between these two organisms. Finally (and this is a methodological difference), we use phase-plane geometry rather than numerical analysis to understand the behavior of the system. For our purposes, the advantage of phase-plane analysis is that it is not necessary to postulate specific dependence of the butterfly growth rate on the ant population density, or ant equilibrium density on butterfly population density. Instead, we can show that the logic of our principal conclusions are generic and depend only on the simplest qualitative properties of these density-dependent functions. Any function that looks like that sketched in figure 2 will lead to solutions that have the same qualitative properties. This is a desirable feature for a biological model, since it is often difficult in nature to measure or even estimate population parameters accurately.

In conclusion, this model describes the population dynamics of mutualistic,

commensal, and parasitic lycaenid-ant interactions and shows that all three of these two-species interactions can be stable in nature. The model may have general applicability to other two-species interactions, such as those between homopterans and ants or between plants and their pollinators. In the latter case, the gametes (pollen and eggs) are again in an ecological niche different from that of the adult plants. Pollinators increase the birth rates by increasing fertilization rates.

Our model does not address the question of how different kinds of two-species interactions might evolve. Pierce (1984) discussed some of the factors that have influenced the evolution of lycaenid-ant associations. Several authors, most notably Axelrod and Hamilton (1981) using game theory and Roughgarden (1975) and Keeler (1981) using cost-benefit analysis, have developed models that predict conditions under which cooperative species interactions could evolve. Wilson (1980) adopted an approach similar to that of May (1976) in developing a series of models to examine the evolution of community welfare as a whole.

SUMMARY

We present a two-species model that describes the population dynamics of mutualistic, commensal, and parasitic interactions between lycaenid butterflies and ants. The lycaenids affect the equilibrium density of their associated ants, whereas the ants influence both the growth rate and the equilibrium density of the butterflies. The model can describe obligate as well as facultative relationships on the part of the lycaenids, and even when the interaction is mutualistic, the model has globally stable equilibria. We suggest that this model has general applicability to other two-species interactions.

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