BEHAVIOR, HETEROGENEITY, AND THE DYNAMICS OF INTERACTING SPECIES[1]

Peter Chesson
*Ecosystem Dynamics Group, Research School of Biological Sciences, Australian National University,
G.P.O. Box 475, Canberra, ACT 2601 Australia*

Michael Rosenzweig
Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA

INTRODUCTION

Behavior affects population dynamics by adding density dependence or modifying it. We define "density dependence" to mean that the per capita growth rate of a population depends on its own density or the densities of other species with which it interacts. Density dependence greatly affects the magnitude and nature of population fluctuations. It also changes the ability of competing species to coexist, and the persistence of predator–prey interactions. Finally, it interacts with environmental factors in various ways.

Density dependence is *linear* whenever the effect of density on the per capita growth rate is proportional to (has a constant ratio with) density or some other factor depending on density. Otherwise density dependence is *nonlinear.* Evidence from various sources implies that the complexity of nature can be explained only if populations and systems of interacting species are commonly density dependent and, indeed, nonlinearly density dependent (Schaffer and Kot 1986, Rosenzweig 1987a, Murdoch and Walde 1989, P. Chesson and N. Huntly, *unpublished manuscript*). As we shall see below, even very simple behaviors can lead to nonlinear density dependences.

Various heterogeneities, such as environmental variability, patchiness, and phenotypic variation, also affect population dynamics (Strong 1986). While their immediate effects may be density independent, heterogeneities interact with density-dependent processes, profoundly modifying their effects while leaving their importance undiminished (Chesson and Huntly 1988, *unpublished manuscript*). As discussed here and elsewhere (Gordon 1991), behavioral responses to environmental variation can link heterogeneity and population dynamics. In various settings we show how behavior can be a response to heterogeneity, introducing nonlinear density dependence and qualitatively altering population dynamics. Also, even simple behaviors can cause *nonadditivity,* which is an interaction between environmental and density-dependent processes. It has a critical effect on the coexistence of competing species.

To understand these various joint effects of behavior and heterogeneity on population dynamics, we first briefly review the general effects of behavior on dynamics by discussing selected examples. We take a broad view of "behavior," defining it as an organism's response to its surroundings. We then consider examples of the various ways in which heterogeneity affects dynamics, and for each example we consider the interaction of behavior with heterogeneity.

BEHAVIOR AND DYNAMICS

Many different sorts of behaviors add nonlinearities to dynamical models, for example, mate choice, habitat selection, oviposition, and feeding behavior. Feeding behavior, which we now discuss in detail, is a basic feature of many population models and provides a convenient demonstration of some general principles.

An important aspect of feeding by predators is the necessity to spend time handling prey. Handling time means that prey consumption must be a nonlinear function of prey density, because as prey density increases, predation becomes limited by the ability to handle prey, and so reaches a maximum absolute number of prey consumed per unit time (Fig. 1a: curves i and ii). In per capita terms, this means a reduced effect of predation on the prey population at higher prey densities (Fig. 1b: curves i and ii) because predators must consume a smaller fraction of the available prey (Taylor 1984, Murdoch and Bence 1987). This reduction occurs more rapidly with larger handling time (Fig. 1b: curve i vs. curve ii).

Fig. 1 shows that the effect of this simple and usually necessary behavior of handling prey is to increase prey per-capita growth rates as a function of prey density, i.e., handling time adds a component of *inverse density dependence* to prey population dynamics. Inverse density dependence arising in this way tends to increase

---

[1] For reprints of this Special Feature, see footnote 1, page 1179.

population fluctuations because a change in prey density causes a change in predation that boosts the change in prey density. Such inverse density dependence may be an important factor in predator–prey cycles (Rosenzweig 1977, May 1981).

Positive, as opposed to inverse, density dependence in feeding behavior also arises. A variety of behavioral models lead to the type III functional response (Holling 1965, Murdoch and Oaten 1975, Hassell 1978, Abrams 1982, Mitchell and Brown 1990) for which the number of prey consumed per unit time accelerates with increases in prey density until handling time begins to limit prey consumption (Fig. 1a: curve iii). This introduces positive density dependence at low prey densities because predation causes reductions in per capita growth rate as prey density increases until the effects of handling time become overriding (Fig. 1b: curve iii). Moderate levels of positive density dependence tend to be stabilizing, because changes in population density are met by counteracting changes in the prey per-capita growth rate. Thus, predator behaviors leading to a type III functional response can have a stabilizing effect at low prey density (Oaten and Murdoch 1975).

Models of optimal behavior suggest even more intricate nonlinearities for the functional response (Abrams 1982). The implications for population dynamics are clearly significant, but as yet incompletely explored. Moreover, to our knowledge, there have been no experiments of the sort that might uncover these more complex functional responses in nature.

As feeding is a basic ingredient in population models, it is not surprising to find that behavior manifested in the functional response has important effects in a variety of other situations also. For example, in community models Abrams (1980) has shown that a consumer's functional response modifies the maximum overlap in resource use that is consistent with species coexistence.

The functional response of a species that shares a predator with other species will likely depend on the densities of these other species. Such multidimensional density dependence can be complex, but often its most important aspect is *frequency dependence*. Frequency dependence is *positive* if a species gains an advantage in per capita population growth by having a low relative abundance. Frequency dependence is *negative* or *inverse* if, instead, a species gains a disadvantage in per capita population growth at low relative abundance.

"Switching" (Murdoch and Oaten 1975), which is a term for positive frequency dependence of functional responses, potentially promotes coexistence of prey species (Roughgarden and Feldman 1975, Comins and Hassell 1976, Holt 1977, Tansky 1978, Abrams 1987a, b), because the advantage gained by a species at low relative density may oppose competitive exclusion.
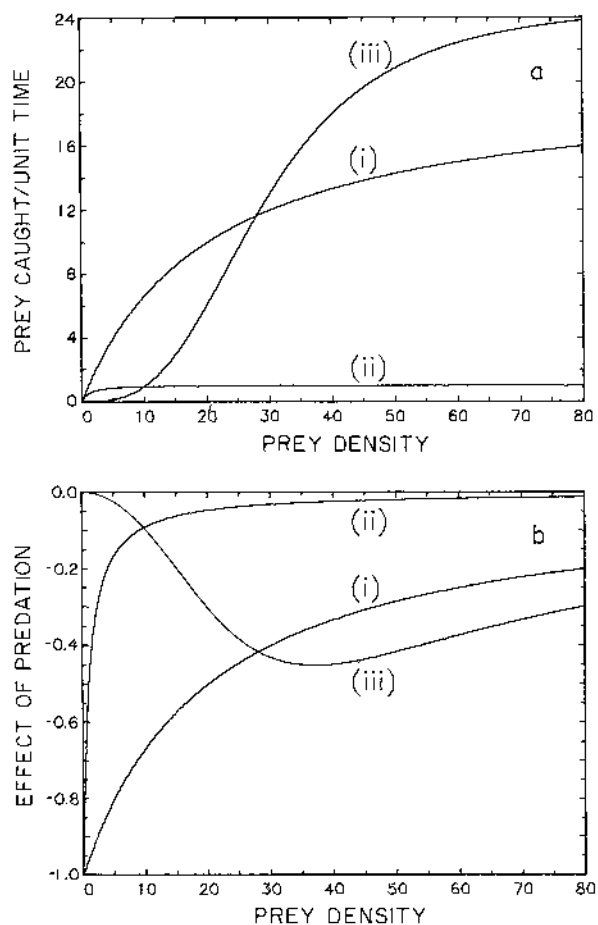

FIG. 1. (a) Functional responses. Curves i and ii: type II responses (Holling 1965) of a predator with respectively small and large values of handling time. Curve iii: type III response. (b) Contributions of predation to prey per-capita growth rate for the three functional responses depicted in (a).

Abrams (1987a, b) has shown how optimal foraging considerations imply switching under some circumstances, but, depending on the relative energy and nutrient contents of the prey, it is possible for negatively frequency dependent foraging to be optimal (Abrams 1987a, b, Abrams and Shen 1989). In some situations such negative frequency dependence may lead to competitive exclusion; in others it leads to large fluctuations in the relative abundances of prey species (Abrams and Shen 1989).

HETEROGENEITY, BEHAVIOR, AND DYNAMICS

We have seen how various behaviors or aspects of behavior can have important dynamical consequences. Behaviors with important dynamical consequences may arise in response to heterogeneity, or their effects may be modified or extended in the presence of heterogeneity. We study these possibilities using several ex-
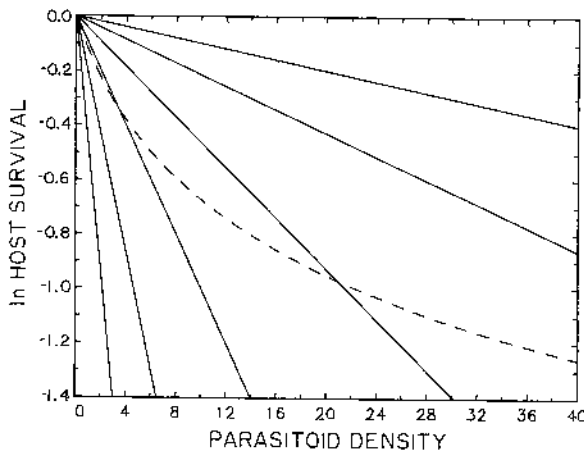
FIG. 2. Host survival as a function of parasitoid density under different random-encounter rates (——, Nicholson-Bailey model), and as an average over the variation in survival rates experienced by all host individuals (– – –, negative binomial model).

amples. In each example, however, we first ask how heterogeneity affects the system. Then we add behavior and see what changes it brings.

Host–parasitoid systems

Like the effects of behavior, the effects of heterogeneity can also be studied in terms of the nonlinearities they induce. In the discrete time models of these systems, linearity of density dependence is best studied on a log scale, due to the multiplicative nature of population growth. The random-encounter model of parasitoids with hosts leads to a negative exponential rate of host survival as a function of parasitoid density, which is linear on a log scale (Fig. 2: solid lines). Variation of the host survival rate in space (Free et al. 1977), or, more generally, from one host individual to another (Chesson and Murdoch 1986), leads to a total system response that is not exponential, and therefore not linear on a log scale (Fig. 2: dashed line). The decline in host survival with parasitoid density is more moderate than exponential and exerts a stabilizing influence (Hassell et al. 1991), because reductions in the host population following the buildup of parasitoid numbers are less severe.

The important heterogeneity in these host–parasitoid systems is in the risk of parasitism to which individual hosts are exposed. Spatial variation in host density can lead to heterogeneity in risk if parasitoids respond behaviorally to local host densities. Parasitoids may aggregate in areas of high host density, generating greater risk in dense patches and lower risk in less-dense patches, tending to stabilize the host–parasitoid interaction (Hassell and May 1974). This is an example where behavior converts otherwise irrelevant

heterogeneity (in host distribution) into heterogeneity with important effects on dynamics (variation in host risk of parasitism). Optimal foraging considerations suggest that parasitoids should indeed concentrate their efforts in patches that have higher numbers of parasitoids (Comins and Hassell 1979, Lessells 1985). However, optimal parasitoid behavior need not lead to maximum stability. Moreover, aggregation in patches of high host density appears far from the most commonly observed behavior in nature (Pacala and Hassell 1991).

Stability could also result from the opposite relationship (a negative spatial relationship) between risk of parasitism and host density (Hassell 1984, Chesson and Murdoch 1986), as variation in host density would still lead to variation in the risk of parasitism. Empirically, lowered risk of parasitism has been found to correspond to high host density in some systems (Lack 1954, Pacala and Hassell 1991). One explanation for this phenomenon is the parasitoid's functional response. If handling time becomes limiting in dense patches of hosts, the individual risk of parasitism will be lower than in other patches (Hassell et al. 1985, Chesson and Murdoch 1986). However, it should be remembered that previously we found handling time to be a destabilizing factor. It seems likely that the net effect of handling time will be destabilizing when host densities vary only a little, but stabilizing in the presence of large variation in host densities (which would mean large variation in risk). This issue needs further study.

Empirical evidence points to large variation in individual host risk in nature, but the above explanations of it cannot apply in most cases because in most cases variation in risk is not related to variation in host density (Pacala and Hassell 1991). Aggregation of parasitoid attacks unrelated to host density could result from existence of host refuges, which make some hosts more difficult to find than others (Bailey et al. 1962), from differences in host phenotypes (Chesson and Murdoch 1986, Pacala and Hassell 1991) or from fluctuations in local parasitoid density due to unstable local population dynamics (Reeve 1988). However, there might also be behavioral explanations for highly mobile parasitoids. What could produce behavior that leads to aggregation independent of host density? Do parasitoids aggregate to some important environmental stimulus, or are they aggregating to each other? The latter could conceivably be the case if there are advantages in numbers for penetrating and finding hosts or host sources.

Predator–prey systems

The similarity between predators and parasitoids (Hassell 1978) suggests that these stabilizing effects of

aggregative behavior, which result from nonlinear host survival as a function of parasitoid density, might apply to the usual sorts of predator–prey systems. Aggregative responses of predators to prey density are known in the field (Turchin and Kareiva 1989). In predator–prey systems, the effects of aggregation have been examined by considering its effects on the functional response, which specifies the prey death rate as a function of prey density.

When predators must spend time traveling between patches of prey, behavior that causes them to spend more time in patches of higher prey density might lead to a type III functional response (Murdoch and Oaten 1975), which could promote stability of the predator-prey interaction. As pointed out by Murdoch and Bence (1987), many aspects of predation, including handling time discussed above (see *Behavior and dynamics*), promote fluctuations. Therefore, one should think of stabilizing factors as reducing population fluctuations, not closely regulating a population about equilibrium. Indeed, this is perhaps the appropriate view of stabilizing factors in most ecological systems.

We have considered so far just the behavioral response of predators to prey, as if prey did not react to predators at all. However, prey can show an enormous variety of responses to predation (Lima and Dill 1990), with the potential for important consequences for dynamics (Ives and Dobson 1987). Habitat selection or movement behavior can sometimes lead to stabilizing dynamics as prey take advantage of refuges within a spatially heterogeneous environment (Rosenzweig and MacArthur 1963), although there can be a variety of complications depending on the nature of these refuges (McNair 1986). The clearest results come from models assuming an absolute refuge, which may be defined as an area chosen preferentially by prey that is inaccessible to predators and has a maximum capacity. The population growth rate for the total of the refuge and nonrefuge populations is very strongly density dependent, with strongly stabilizing properties (Murdoch and Oaten 1975, Taylor 1984, McNair 1986, Sih 1987). An especially interesting example has been provided recently by Taylor and Pekins (1990) who showed that the boundaries between wolf territories provide the prey refuge that ultimately has the stabilizing effect.

The most complex case, and perhaps the most common in nature, is where predators and victims must solve simultaneously their individual problems of optimal spatial distribution in a heterogeneous landscape. Schwinning and Rosenzweig (1990) showed in a three-species model that a joint optimal solution may be impossible. In such circumstances, selection pressures are in continuous flux depending on the behavioral strategies of other species and their population densities. Population dynamic processes can be expected to be continually changing in response to changes in behavioral strategies.

Spatial heterogeneity and competitive relationships

Heterogeneity has a remarkable tendency to create frequency dependence in models of competing species (Levin 1974, Comins and Noble 1985, Ives 1988, Chesson and Huntly 1989). Different situations with no frequency dependence (dominance at all densities by some species over others), when combined, may yield frequency dependence, which will oppose competitive exclusion and maintain diversity. Heterogeneity may in some circumstances give rise to inverse frequency dependence that hastens competitive exclusion and lowers diversity (Chesson and Huntly 1988). However, provided competition occurs on a local spatial scale, spatial heterogeneity seems almost inevitably to give rise to frequency dependence that maintains diversity (Chesson 1985).

Behavior can greatly magnify this coexistence-promoting effect of spatial heterogeneity. Isoleg theory shows how habitat selection by competitors can take account of competition both within and between species (Rosenzweig 1981, 1985). If species vary in their competitive abilities between habitats, habitat selection will generally favor species being more strongly segregated than one would expect simply on the basis of variation in population growth rates between habitats. Thus, behavior can reinforce existing heterogeneities, creating very strong nonlinearities and greatly enhancing opportunities for coexistence.

If individuals of a species achieve their highest fitnesses in different habitats from other species, and individuals cannot judge the value of a particular patch of habitat except by using it, the species should segregate into distinct habitats. Such behavioral segregation has been called "the ghost of competition past" (Brown and Rosenzweig 1986). But it is not uncommon in nature for there to be some habitats that are favored over other habitats by all species ("centrifugal" habitat organization, Rosenzweig and Abramsky 1986, Keddy 1990, Keddy and MacLellan 1990). A strict segregation of species does not then result, but flexible use of marginal habitat by species still has a major coexistence-promoting effect.

A variation on these ideas is to consider indirect interactions between species that result from sharing a predator, rather than sharing common resources as the examples above assume. The behavior of the predator adds an extra element, and Holt (1984) shows that optimal foraging by the predator can lead to nonlinearities that promote coexistence of prey species. Without this behavioral flexibility of the predator in the

presence of spatial variation in prey density, exclusion of prey species by apparent competition is predicted.

Temporal heterogeneity and competitive relationships

Temporal heterogeneity means that consistent trends in population growth may not be evident on a short time scale but appear on a longer time scale (Chesson and Huntly 1989). Thus, we must take a long-term view of frequency dependence, asking whether a species at low relative density gains an advantage in the long run and tends to increase, or instead tends to decline toward extinction in the long run. The conditions for frequency dependence to arise with temporal heterogeneity are stricter than those for spatial heterogeneity (Chesson 1985) and depend more intricately on features of the system. There are two broad cases. For each of these, we first describe their general properties and then go on to define how behavior contributes to them.

Nonlinear competitive factors. — Per capita population growth rates of different species may be nonlinearly related to a common measure of the intensity of competition (Fig. 3). The growth rates are curved in relation to each other and may cross in one or more places. Fig. 3 illustrates how frequency dependence can arise with such relatively nonlinear growth rates in the presence of temporal heterogeneity in competition. Species ii has a higher growth rate than species i for competition within the intermediate range between the intersections of the two curves. Species i has the higher growth rate outside this range. If competition fluctuates within the intermediate range of values when species ii is at low density, species ii will be advantaged and will increase from low relative density. If competition fluctuates mostly outside the intermediate range when species i is at low relative density, species i will be advantaged at low relative density and will increase, at least in the long run. In these circumstances, the system is frequency dependent, and competitive exclusion is opposed.

That scenario fits the model of two consumers competing for a common biological resource proposed by Armstrong and McGehee (1980). In their model the relative nonlinearity depicted in Fig. 3 comes about because species ii has the larger handling time for the resource, whose abundance can be taken as an inverse measure of the amount of competition. Also, the larger handling time of species ii means that when it is at high relative abundance (and species i is therefore at low relative abundance), there are larger fluctuations in resource levels and hence larger fluctuations in competition due to the destabilizing effect that a large handling time has on the consumer–resource interaction,

as discussed above (see *Behavior and dynamics*) for predator–prey interactions.

Such nonlinear per-capita growth rates coupled with fluctuations in competition that depend on species relative abundances provide a general mechanism of coexistence (Levins 1979, Armstrong and McGehee 1980, Brown 1989a). This mechanism can rely on differences in quantitative measures of behavior, such as the handling time arising in the example due to Armstrong and McGehee (1980). The example due to Brown (1989a) involves a switch from feeding to not feeding ("dormancy") when resource levels are too low to make feeding profitable. Here relatively nonlinear per-capita growth rates arise from differences between the species in the resource level that triggers the switch from feeding to dormancy.

Interactions between environment and competition. — If species do not have relatively nonlinear per-capita growth rates as functions of competition, temporal fluctuations can still promote coexistence provided three conditions are met (Chesson and Huntly 1989). These conditions, which we now state, constitute a definition of distinct temporal niches for different species. First, the different species must be favored by different sorts of environmental conditions that fluctuate over time. Second, environmental fluctuations must translate into fluctuations in competition. Third, there must be an interaction between environmental and competitive factors.

Without the interaction between environmental and competitive factors, the gains that a species makes during periods when it is favored by environmental and competitive factors could be canceled by losses incurred during poor conditions favoring its competitors.

Interactions between environmental and competitive factors can be recognized by plotting the growth rate against the intensity of competition under different environmental conditions (Fig. 4). Interactions exist whenever these curves are not parallel (Fig. 4b and c). The subadditive case (Fig. 4b) is generally associated with frequency dependence that promotes coexistence (Chesson and Huntly 1989). In the subadditive case, the lower response to competition (shallower slope of the growth rate) under poor environmental conditions means that the combination of relatively poor environmental and competitive conditions for a species cannot eliminate the gains achieved under good environmental conditions and low competition. In contrast, in the superadditive case of Fig. 4c, poor conditions can more than eliminate the gains of good conditions in such a way that inverse frequency dependence and competitive exclusion result from a fluctuating environment.

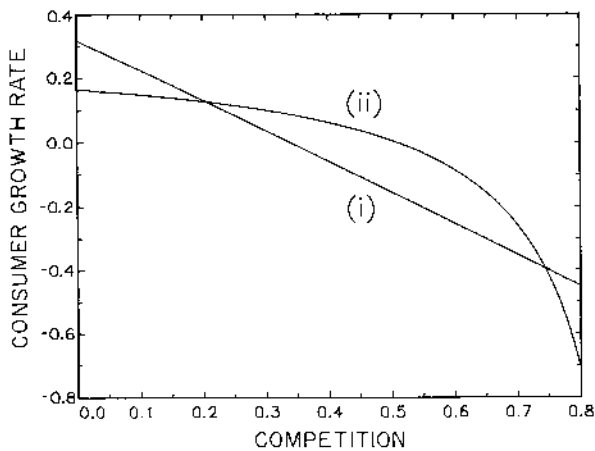An early suggestion for the origin of subadditive growth rates involved the storage effect or the buffering

FIG. 3. Growth rates of two consumer species as functions of the amount of competition, measured as the inverse of resource availability. The curve for species i is almost linear, while the curve for species ii is strongly nonlinear. Thus, the two curves are nonlinearly related to each other.

effect on population growth rates that results when the adults of a population are long lived and have survival rates relatively insensitive to environmental and competitive factors, while reproduction and juvenile survival are highly sensitive to these factors (Chesson and Huntly 1988).

Behavior can lead to nonadditive growth rates in several different ways. Abrams (1984) suggested that a fluctuating environment might cause fluctuations in the capture rates of resources, for given resource abundances. If functional responses are nonlinear due to a handling-time limitation, a superadditive interaction results, causing inverse frequency dependence, which promotes competitive exclusion (Chesson 1988).

Subadditivity arises directly from the dormancy behavior that Brown (1989b) established for a desert rodent community. In Brown's example, which comes from a careful empirical study, there is some seasonal separation of rodent species in foraging efficiency. Some species become dormant during periods when foraging is poor. Dormancy buffers a population against poor environmental and competitive conditions, giving subadditivity and promoting coexistence.

Both subadditive and superadditive growth rates potentially arise from habitat selection. Just as juveniles and adults may show different sensitivities to environmental and competitive factors, individuals occupying different microhabitats may not be equally sensitive to environmental and competitive factors. Consider, for example, poikilothermic organisms that live in shaded or sunny microhabitats (e.g., occupants of pitcher plants or bromeliads that can be shaded to varying degrees, Istock and Weisburg 1987). The shaded microhabitats offer less exposure to the weather and therefore less
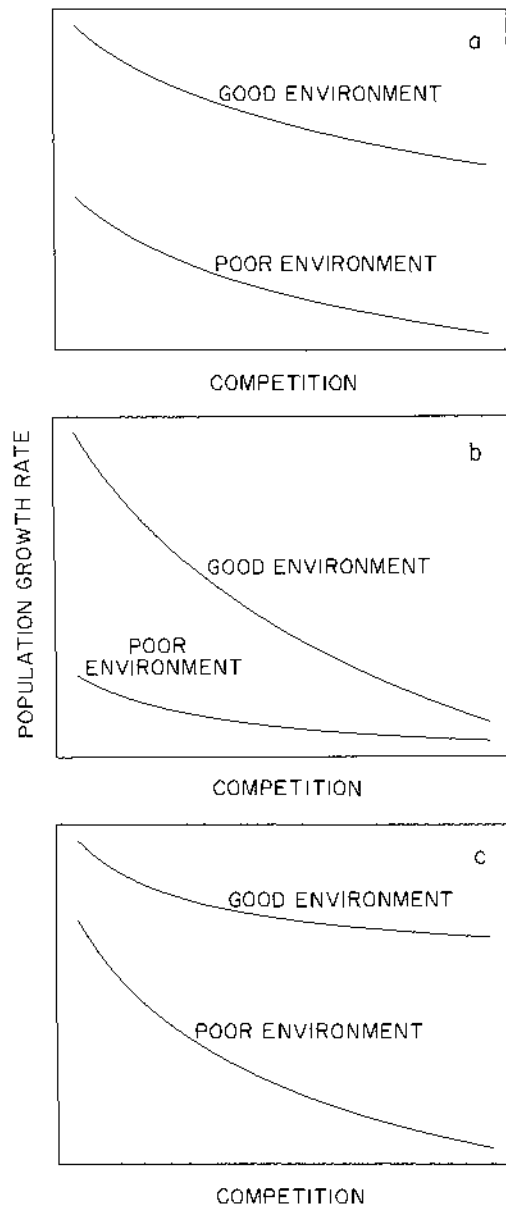

FIG. 4. Growth rates of a population as a function of competition under different environment conditions. (a) No interaction between environment and competition (additive case). (b) Negative interaction between environment and competition (subadditive). (c) Positive interaction between environment and competition (superadditive).

sensitivity to weather conditions. In addition, by being generally cooler, individual organisms may grow less quickly and deplete resources less in these shaded places. Organisms in the shaded microhabitat therefore experience competition less; we can think of them as less sensitive to competition.

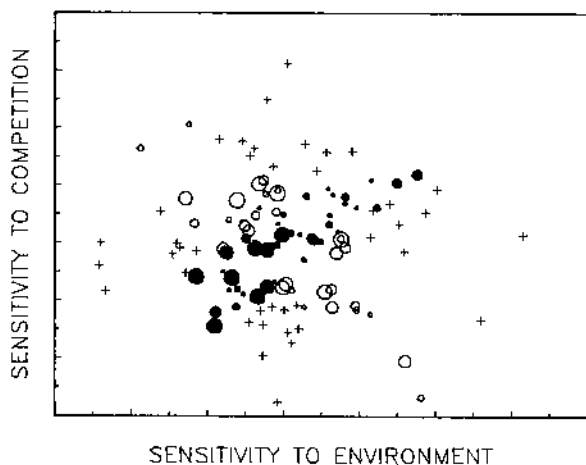The relatively stable population growth processes in the shaded microhabitat of this example buffer pop-

FIG. 5. Scatter plot of available microhabitats. Filled circles: subset giving a postive correlation between environmental and competitive sensitivities. Open circles: subset with negative correlation. Pluses: habitats not chosen in either of the previous cases. The area of the circle represents the importance of a microhabitat to population growth and hence the weight given to the microhabitat in calculating the correlation.

ulation growth against unfavorable environmental and competitive conditions, while the organisms living in the sunny habitat may be able to show strong population growth at times of low competition and favorable environment. Such favorable environmental conditions coupled with low competition would be expected if the species is currently at low density, and the favorable environmental conditions that it experiences do not favor its competitors. Occupancy of both these microhabitats means that the population can respond well under favorable environmental and competitive conditions but does not suffer too severely under unfavorable conditions. Thus the growth rate of the population is subadditive.

This example works because sensitivity to environment and competition is positively correlated across microhabitats (shaded places have lower sensitivity to both environmental and competitive factors than sunny places). If the correlation were negative, superadditive growth rates would result. Additive growth rates result from no correlation (Chesson 1990).

The correlation between the sensitivities to environmental and competitive factors across microhabitats is profoundly influenced by habitat selection. Each microhabitat must be weighted in the correlation calculation by the contribution to total population growth from the subpopulation in a particular microhabitat (Chesson 1990). In Fig. 5, microhabitats are shown with no correlation between the sensitivities to competition and environment if they are chosen at random. Two potential nonrandom outcomes of habitat selec-

tion are represented, one giving a positive correlation, the other a negative correlation.

We have no information at present, either theoretical or empirical, on habitat selection in relation to sensitivities to environmental and competitive factors. A positive correlation, however, seems to correspond to a situation very much akin to bet hedging. Therefore, following standard theoretical arguments for the evolution of bet-hedging strategies (Levin et al. 1984, Bulmer 1985, Ellner 1985), one might expect a positive correlation to be favored by natural selection. Virtually no one has looked to see whether this expectation is true in nature. If it is, we should expect the outcome of habitat selection often to be subadditivity, which will lead to positive frequency dependence and will promote coexistence in a temporally fluctuating environment.

The discussion above does not take account of the fact that habitat selection could be density dependent. In that case, all of its effects are magnified. A species at low density can select habitats on the basis of another species' density without being restricted by its own density. An outcome of this is that species do not need separate environmental niches for the interaction between environment and competition to be effective. Other small differences between the species, which become magnified by environmental effects, come into play. The system response is strongly frequency dependent, enabling coexistence (P. Chesson and M. Rosenzweig, *unpublished manuscript*).

CONCLUSIONS

Organisms often behave selectively in heterogeneous situations. It should not be surprising therefore to find interesting behaviors associated with heterogeneity that create their own effects at the population level, such as the type III functional response. We should be similarly unsurprised to find that behavior can magnify the effects of existing heterogeneity or transfer that heterogeneity from the environment to the population or from one population to another, as we have seen in host–parasitoid, predator–prey, and competitive systems reviewed above. Even relatively inflexible behavior can perform these sorts of functions, as we have seen in the various situations in which the time taken to handle prey has major significance for population dynamics and species interactions.

It is interesting to speculate, however, on the possibilities arising as behavior becomes more flexible. Greater similarity of behavior within species vs. between species may lead to frequency-dependent effects that promote coexistence, as we have seen in several examples involving habitat selection. The more flexible the behavior, the more strongly coexistence is promoted, as we have seen when habitat selection has been

made responsive to density and not just to environmental factors. Much of the effect is due to greater opportunities available to individuals of less abundant species, because not so many other individuals make the same choice and compete with them.

It is natural to expect strong links between population dynamics and behavior, as we have reviewed above. Population dynamics are determined by per capita growth rates. Natural selection takes place through fitness differences, which in population genetics models (e.g., Crow and Kimura 1970) are differences in per capita growth rates of different genotypes, favoring at any time the genotype with the highest per-capita growth rate. Evolution of behavior should, as a matter of course, lead to alteration of per capita population growth rates. Thus, important links between behaviors and population dynamics are to be expected.

Consideration of optimality and evolutionarily stable stategies (Maynard Smith 1978, Rosenzweig 1987b) indicates behaviors presumed to represent end points of natural selection. It is but a short step to enquire about the per capita population growth rate associated with an end-point behavior, because this per capita growth rate is also the end point of natural selection under the circumstances of the optimization procedure. Likewise, empirical studies of the benefits of behaviors lead to information about dynamics through the link between the benefits accrued and subsequent population growth. This link can be exploited explicitly to yield dynamical information by measuring behavior. For example, Abramsky et al. (1991) use habitat selection to measure isoclines of desert rodents. We believe these links can be investigated to a much greater degree than at present to yield information of great benefit to the understanding of population dynamics and species interactions.

LITERATURE CITED

Abrams, P. A. 1980. Consumer functional response and competition in consumer-resource systems. Theoretical Population Biology 17:80–102.
———. 1982. Functional response of optimal foragers. American Naturalist 120:382–390.
———. 1984. Variability in resource consumption rates and the coexistence of competing species. Theoretical Population Biology 25:106–124.
———. 1987a. The functional response of adaptive consumers of two resources. Theoretical Population Biology 32:262–288.

———. 1987b. Indirect interactions between species that share a predator: varieties of indirect effects. Pages 38–54 in W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.
Abrams, P. A., and L. Shen. 1989. Population dynamics of systems with consumers that maintain a constant ratio of intake rates of two resources. Theoretical Population Biology 35:51–89.
Abramsky, Z., M. L. Rosenzweig, and B. Pinshow. 1991. The shape of a gerbil isocline measured using principles of optimal habitat selection. Ecology 72:329–340.
Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. American Naturalist 115:151–170.
Bailey, V. A., A. J. Nicholson, and E. J. Williams. 1962. Interactions between hosts and parasites when some hosts are more difficult to find than others. Journal of Theoretical Biology 3:1–18.
Brown, J. S. 1989a. Coexistence on a seasonal resource. American Naturalist 133:168–182.
———. 1989b. Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs 59:1–20.
Brown, J. S., and M. L. Rosenzweig. 1986. Habitat selection in slowly regenerating environments. Journal of Theoretical Biology 123:151–171.
Bulmer, M. G. 1985. Selection for iteroparity in a variable environment. American Naturalist 126:63–71.
Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theoretical Population Biology 28:263–287.
———. 1988. Interactions between environment and competition: how fluctuations mediate coexistence and competitive exclusion. Pages 51–71 in A. Hastings, editor. Community ecology. Lecture Notes in Biomathematics 77. Springer-Verlag, New York, New York, USA.
———. 1990. Geometry, heterogeneity and competition in variable environments. Philosophical Transactions of the Royal Society of London, Series B 330:165–173.
Chesson, P., and N. Huntly. 1988. Community consequences of life-history traits in a variable environment. Annales Zoologici Fennici 25:5–16.
Chesson, P., and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. Trends in Ecology and Evolution 4:293–298.
Chesson, P. L., and W. W. Murdoch. 1986. Aggregation of risk: relationships among host–parasitoid models. American Naturalist 127:696–715.
Comins, H. N., and M. P. Hassell. 1976. Predation in multiprey communities. Journal of Theoretical Biology 62:93–114.
Comins, H. N., and M. P. Hassell. 1979. The dynamics of optimally foraging predators and parasitoids. Journal of Animal Ecology 48:335–351.
Comins, H. N., and I. R. Noble. 1985. Dispersal, variability and transient niches: species coexistence in a uniformly variable environment. American Naturalist 126:706–723.
Crow, J. F., and M. Kimura. 1970. An introduction to population genetics theory. Burgess, Minneapolis, Minnesota, USA.
Ellner, S. 1985. ESS germination strategies in randomly varying environments. I. Logistic-type models. Theoretical Population Biology 28:50–79.
Free, C. A., J. R. Beddington, and J. H. Lawton. 1977. On the inadequacy of simple models of mutual interference for parasitism and predation. Journal of Animal Ecology 46:543–554.

Gordon, D. 1991. Behavioral flexibility and the foraging ecology of seed-eating ants. American Naturalist, *in press*.

Hassell, M. P. 1978. The dynamics of arthropod predator–prey systems. Princeton University Press, Princeton, New Jersey, USA.

———. 1984. Parasitism in patchy environments: inverse density dependence can be stabilizing. IMA Journal of Mathematics Applied in Medicine and Biology 1:123–133.

Hassell, M. P., C. M. Lessells, and G. C. McGavin. 1985. Inverse density dependent parasitism in a patchy environment: a laboratory system. Ecological Entomology 10:393–402.

Hassell, M. P., and R. M. May. 1974. Aggregation in predators and insect parasites and its effects on stability. Journal of Animal Ecology 42:567–594.

Hassell, M. P., R. M. May, S. W. Pacala, and P. L. Chesson. 1991. The persistence of host–parasitoid associations in patchy environments. I. A general criterion. American Naturalist, *in press*.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada 45:1–60.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

———. 1984. Spatial heterogeneity, indirect effects, and the coexistence of prey species. American Naturalist 124:377–406.

Istock, C. A., and W. G. Weisburg. 1987. Strong habitat selection and the development of population structure in the mosquito. Evolutionary Ecology 1:348–362.

Ives, A. R. 1988. Covariance, coexistence and the population dynamics of two competitors using a patchy resource. Journal of Theoretical Biology 133:345–361.

Ives, A. R., and A. P. Dobson. 1987. Antipredator behavior and the population dynamics of simple predator–prey systems. American Naturalist 130:431–447.

Keddy, P. A. 1990. Competitive hierarchies and centrifugal organization in plant communities. Pages 265–290 *in* J. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, New York, New York, USA.

Keddy, P. A., and P. MacLellan. 1990. Centrifugal organization in forests. Oikos 59:75–84.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon, Oxford, England.

Lessells, C. M. 1985. Parasitoid foraging: should parsitism be density dependent? Journal of Animal Ecology 54:27–41.

Levin, S. A. 1974. Dispersion and population interactions. American Naturalist 108:207–228.

Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. Theoretical Population Biology 26:165–191.

Levins, R. 1979. Coexistence in a variable environment. American Naturalist 114:765–783.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

May, R. M. 1981. Models for two interacting populations. Pages 78–104 *in* R. M. May, editor. Theoretical ecology. Second edition. Sinuaer, Sunderland, Massachusetts, USA.

Maynard Smith, J. 1978. Optimization theory in evolution. Annual Review of Ecology and Systematics 9:31–56.

McNair, J. N. 1986. The effects of refuges on predator–prey interactions: a reconsideration. Theoretical Population Biology 29:38–63.

Mitchell, W. A., and J. S. Brown. 1990. Density-dependent harvest rates by optimal foragers. Oikos 57:180–190.

Murdoch, W. W., and J. Bence. 1987. General predators and unstable prey populations. Pages 17–30 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hannover, New Hampshire, USA.

Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1–131.

Murdoch, W. W., and S. J. Walde. 1989. Analysis of insect population dynamics. Pages 113–140 *in* J. Whitaker and P. J. Grubb, editors. Toward a more exact ecology. British Ecological Society Symposium Volume. Blackwell Scientific, Oxford, England.

Oaten, A., and W. W. Murdoch. 1975. Functional response and stability in predator–prey systems. American Naturalist 109:289–298.

Pacala, S. W., and M. P. Hassell. 1991. The persistence of host–parasitoid associations in patchy environments. II. Evaluation of field data. American Naturalist, *in press*.

Reeve, J. D. 1988. Environmental variability, migration, and persistence in host–parasitoid systems. American Naturalist 132:810–836.

Rosenzweig, M. L. 1977. Aspects of biological exploitation. Quarterly Review of Biology 52:371–380.

———. 1981. A theory of habitat selection. Ecology 62:327–335.

———. 1985. Some theoretical aspects of habitat selection. Pages 517–540 *in* M. L. Cody, editor. Habitat selection in birds. Academic Press, New York, New York, USA.

———. 1987a. Community organization from the point of view of habitat selectors. Pages 469–490 *in* J. H. R. Gee, and B. J. Giller, editors. Organization of communities: past and present. British Ecological Society Symposium number 27. Blackwell Scientific, Oxford, England.

———. 1987b. Habitat selection as a source of biological diversity. Evolutionary Ecology 1:315–330.

Rosenzweig, M. L., and Z. Abramsky. 1986. Centrifugal community organization. Oikos 46:339–348.

Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator–prey interactions. American Naturalist 97:209–223.

Roughgarden, J., and M. Feldman. 1975. Species packing and predation pressure. Ecology 56:489–492.

Schaffer, W. W., and M. Kot. 1986. Chaos in ecological systems: the coals that Newcastle forgot. Trends in Ecology and Evolution 1:58–63.

Schwinning, S., and M. L. Rosenzweig. 1990. Periodic oscillations in an ideal-free predator–prey distribution. Oikos 59:85–91.

Sih, A. 1987. Prey refuges and predator–prey stability. Theoretical Population Biology 31:1–12.

Strong, D. R. 1986. Density vagueness: abiding the variance in the demography of real populations. Pages 257–268 *in* J. Diamond and T. Case, editors. Community ecology. Harper & Row, New York, New York, USA.

Tansky, M. 1978. Switching effect in prey–predator system. Theoretical Population Biology 70:263–271.

Taylor, R. J. 1984. Predation. Chapman and Hall, New York, New York, USA.

Taylor, R. J., and P. J. Pekins. 1990. Territory boundary avoidance as a stabilizing factor in wolf–deer interactions. Theoretical Population Biology, *in press*.

Turchin, P., and P. Kareiva. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. Ecology 70:1008–1016.