

NOTES AND COMMENTS

ARGUMENTS IN FAVOR OF HIGHER ORDER INTERACTIONS

A higher order interaction occurs whenever one species affects the nature of the interaction between two others. There has been considerable controversy over whether there are higher order interactions in competitive guilds of three or more species. A recent article by Pomerantz (1981) shows that previous experiments widely cited as demonstrating the existence of higher order interactions, are actually consistent with the hypothesis that there are no higher order interactions, but there are nonlinear intraspecific density-dependent effects. I agree that the present experimental evidence for higher order interactions is weak. There are, however, some strong deductive arguments for believing that many competitive systems will have higher order interactions; these arguments are reviewed below.

Competitive systems are usually abstractions of consumer-resource systems with several consumers and several resources (Schaffer 1981). If resource population dynamics occur on a sufficiently faster time scale than the consumer population dynamics, it is possible to assume that resource populations are at steady-state values (Schaffer 1981). This result means that competition between consumers can be described without explicit consideration of resource dynamics; resource dynamics will, however, determine the form of the consumer population growth equations. Mechanistic competition models that are derived in this way allow one to relate general features (such as nonlinear density dependence or higher order interactions) to specific assumptions regarding resource utilization.

The Lotka-Volterra competition equations may be derived in the manner described above by assuming that consumers with linear functional responses utilize resources with logistic growth (MacArthur 1970, 1972; Schoener 1974; Lawlor 1980; Abrams 1980*a*). Unfortunately, most resources do not have logistic growth. Pomerantz (1981) notes that nonlinearities in intraspecific density dependence have been observed quite often. Schoener (1973), Harper (1977), and Pomerantz et al. (1980) reviewed studies of density-dependent population growth, and concluded that per capita rates of increase are usually not linear functions of population size. In addition, linear functional responses are relatively uncommon (Hassell 1978; Abrams 1980*b*). This evidence suggests that exploitation competition generally involves nonlinear density dependence and nonconstant competition coefficients (Abrams 1980*a*).

Mechanistic models of exploitative competition of the sort described above also suggest that higher order interactions should generally be observed in multi-species competition systems. Consider a system in which a number of consumer species compete because of overlapping utilization of a set of resource species. A relatively general model for the resource population dynamics in such a system consists of differential equations of the following form:

$$dR_i/dt = R_i f_i(R_i) - \sum_j c_{ij} N_j R_i. \quad (1)$$

The competing consumer species (with population densities N_j) are assumed to have functional responses to resource density (R_i) given by $c_{ij}R_i$. If the functional responses are linear (type 1), the c_{ij} will be constants. $f_i(R_i)$ is the function describing the per capita growth rate of resource i in the absence of consumption; it is a nonincreasing function of resource density. Steady-state resource densities are obtained by setting $dR_i/dt = 0$, and solving; these densities will be denoted \bar{R}_i . It can be shown (e.g., Abrams 1980a) that if per capita population growth rates are solely functions of resource consumption rates, the competition coefficient giving the effect of species k on species j , relative to j on itself is

$$\alpha_{jk} = \frac{\frac{\partial}{\partial N_k} \left(\sum_i c_{ij} \bar{R}_i \right)}{\frac{\partial}{\partial N_j} \left(\sum_i c_{ij} \bar{R}_i \right)}. \quad (2)$$

The numerator in this expression is a measure of interspecific density dependence and the denominator is a measure of intraspecific density dependence. Higher order interactions occur if α_{jk} is a function of any N_m for $m \neq j, k$.

If all of the f_i are linear functions of the R_i (as in logistic growth), and if the c_{ij} are constants (linear functional responses), α_{jk} will be a constant, and the competition coefficient will not be a function of the population densities of any of the species of consumer. Violation of either of these assumptions will usually result in higher order interactions.

Consider first the case of nonlogistic resource growth and linear functional response. Expression (2) will then involve partial derivatives of the \bar{R} with respect to the N . These may be found by implicit differentiation of the expressions for steady-state resource density. (These are found by setting $dR_i/dt = 0$ in expression [1].) Substituting for these quantities in (2) results in the following expression for α_{jk} .

$$\alpha_{jk} = \frac{\sum_i [c_{ij} c_{ik} f'_i(R_i)]}{\sum_i [c_{ij}^2 f'_i(R_i)]}. \quad (3)$$

Here $f'_i(R_i)$ is the partial derivative of f_i with respect to R_i evaluated at steady-state densities. If some of the f_i are nonlinear, some of the f'_i will be functions of \bar{R}_i , which in turn is a function of the population densities of all of the species which consume that resource. Abrams (1980a) gives an explicit formula for expression (3) for the specific case in which f has the form of Gilpin's theta-logistic model (Gilpin and Ayala 1973).

Expression (3) shows that the results of nonlinearity of the f_i are that: (1) intraspecific density-dependent effects will be nonlinear (i.e., the denominator of [3] is not constant); (2) interspecific density-dependent effects will be nonlinear (i.e., the numerator of [3] is not constant); and (3) α_{jk} will not in general be constant. More specifically, α_{jk} will be a function of the population densities of consumer species other than j and k , so that higher order interactions will occur. The only exceptions to the rule of higher order interactions are the trivial cases of no resource overlap with other species or identical competitors. This analysis shows that in this model nonlinear interactions and higher order interactions should either both occur or both not occur; higher order interactions and nonlinear effects are both general consequences of exploitative competition for resources with nonlogistic growth.

The second case to consider is that of nonlinear functional responses. If functional responses are nonlinear, the c_{ij} will be functions of the density of resource i and generally of other resources as well. This could result because time spent handling resources other than i affects the consumption rate of i . Switching behavior can also result in c_{ij} depending on the populations of resources other than i . In this case, the expression for the competition coefficient becomes very complex. However, it is possible to show that higher order interactions will occur without writing out the counterpart of expression (3). The numerator of α_{jk} is

$$-\frac{\partial}{\partial N_k} (\sum_m c_{mj} \bar{R}_m). \quad (4)$$

This can be expanded to

$$\sum_m c_{mj} \frac{\partial \bar{R}_m}{\partial N_k} + \sum_m \frac{\partial c_{mj}}{\partial N_k} \bar{R}_m. \quad (5)$$

The partial derivatives of c_{mj} with respect to N_k can be further expanded as follows

$$\frac{\partial c_{mj}}{\partial N_k} = \sum_i \frac{\partial c_{mj}}{\partial \bar{R}_i} \frac{\partial \bar{R}_i}{\partial N_k}. \quad (6)$$

In general, every term in (4) will be a function of the population densities of species j , k , and other species. This is a result of the fact that both the \bar{R} and the $\partial \bar{R} / \partial N$ will generally be functions of the population densities of all of the species which consume those resources. This shows that other species generally alter the effect of k on j 's population growth rate. An analogous argument shows that other species alter j 's effect on itself. Population densities do not, in general, cancel out of the expression for the competition coefficient. As in the previous case, the same factor (here, nonlinear functional responses) leads to nonlinear interspecific density-dependent effects, nonlinear intraspecific effects, and higher order interactions. All three effects are consequences of the nonlinear dependence of steady-state resource densities on the population densities of resource consumers.

The situation considered thus far is exploitative competition. Competition need not be purely exploitative, but the diversity of possible interference mechanisms prevents a similarly general treatment of interference competition. Interference, however, is generally thought to be an evolutionary response to exploitative

competition (Case and Gilpin 1974), and some element of exploitation is probably present in most competitive systems. This would lead to some higher order effects, based on the argument above.

It should be noted that this argument says nothing about the magnitude of the higher order interactions. It is possible that they are sufficiently small to be ignored for most purposes. The magnitudes of the effects depend on the biological details (resource growth equations, functional responses, consumer population densities) of the system being considered.

The above discussion has some implications for the philosophical issues raised by Pomerantz (1981). He suggests that the assumption of nonlinear intraspecific effects and linear interspecific effects have conceptual priority over the assumption that both types of effects are nonlinear. Further, he suggests that the assumption of nonlinear effects and no higher order interactions should have conceptual priority over the assumption that both types of effects are present. Mechanistic models suggest that the same biological phenomena (nonlinear density dependence in resource population growth and nonlinear functional responses) will lead to all three features: nonlinear intraspecific density dependence, nonlinear interspecific density dependence, and higher order interactions. Assumptions which are given "conceptual priority" should be consistent with what is known about possible mechanisms of competition. I would suggest rejecting Pomerantz's priorities on this basis.

Pomerantz (1981) does provide reasons why higher order effects may be difficult to detect, even in laboratory situations. It seems likely that relatively few field systems will be sufficiently tractable so that manipulation experiments can provide conclusive evidence for or against higher order interactions. Field studies of the mechanism of competition combined with deductive arguments of the sort outlined here seem more likely to provide evidence for or against higher order interactions in specific systems.

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LITERATURE CITED

- Abrams, P. A. 1980a. Are competition coefficients constant? Inductive versus deductive approaches. *Am. Nat.* 116:730-735.
- . 1980b. Consumer functional response and competition in consumer-resource systems. *Theor. Popul. Biol.* 17:80-102.
- Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. *Proc. Natl. Acad. Sci. USA* 71:3073-3077.
- Gilpin, M. E., and F. J. Ayala. 1973. Global models of growth and competition. *Proc. Natl. Acad. Sci. USA* 70:3590-3593.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, New York.
- Hassell, M. P. 1978. *Arthropod predator-prey systems*. Princeton University Press, Princeton, N.J.

- Lawlor, L. R. 1980. Overlap, similarity, and competition coefficients. *Ecology* 61:245–251.
- MacArthur, R. H. 1970. Species packing and competitive equilibria for many species. *Theor. Popul. Biol.* 1:1–11.
- . 1972. *Geographical ecology*. Harper & Row, New York.
- Pomerantz, M. J. 1981. Do “higher order interactions” in competition systems really exist? *Am. Nat.* 117:583–591.
- Pomerantz, M. J., W. R. Thomas, and M. E. Gilpin. 1980. Asymmetries in population growth regulated by intraspecific competition: empirical studies and model tests. *Oecologia* 47:311–322.
- Schaffer, W. M. 1981. Ecological abstraction: the consequences of reduced dimensionality in ecological models. *Ecol. Monogr.* 51:383–401.
- Schoener, T. W. 1973. Population growth regulated by intraspecific competition for energy and time. *Theor. Popul. Biol.* 4:56–84.
- . 1974. Some methods for calculating competition coefficients from resource utilization spectra. *Am. Nat.* 108:332–340.

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