

### ARE COMPETITION COEFFICIENTS CONSTANT? INDUCTIVE VERSUS DEDUCTIVE APPROACHES

One measure of the strength of a competitive interaction between two species is the competition coefficient (usually denoted by  $\alpha_{ij}$ ). This is defined as the ratio of the effect of an individual of species  $j$  on the per capita rate of increase of species  $i$  relative to the effect of an individual of species  $i$  on the per capita rate of increase of its own species (Schoener 1974). In the Lotka-Volterra model of competing species, the competition coefficient is a constant, and therefore independent of the density of species  $i, j$ , or that of any other species in the community. Studies on *Drosophila* species (Ayala et al. 1973), microcrustaceans (Neill 1974), and an amphibian (*Rana*, *Ambystoma*) community (Wilbur 1972) have shown that competition coefficients are not independent of population densities in these communities. Smith-Gill and Gill (1978) have recently provided another example in which the assumption of a constant ratio of inter- to intraspecific competition appears to be inadequate. From their study and the others listed above, they draw the conclusion that "linear approximations of competition coefficients are probably insufficient and misleading," (p. 568). This is clearly an inductive conclusion, based on a very limited number of studies on a small number of species.

If one had to predict whether a model with constant competition coefficients was likely to be adequate for describing a given competitive community on the basis of results from other communities, it would be desirable to have a much larger data base than the studies mentioned in the previous paragraph. Any given competitive community is likely to differ from the ones studied thus far in some significant respect. For example, one might argue that birds are more likely to display constant competition coefficients because they lack the size of age-specific effects that appear to be present in the studies reviewed above. Smith-Gill and Gill apparently were aware of this problem and stated that "... we considered the deductive approach more powerful than inductive experimentation," (p. 558). Nevertheless, their approach is clearly inductive. I will suggest in this note that it is possible to apply a deductive approach to the question of whether the ratio of inter- to intraspecific competition between two given species is likely to be independent of population densities. The conclusion reached here is, however, similar to that of Smith-Gill and Gill; i.e., competition coefficients are likely to be functions of population densities.

Whether or not a model with constant competition coefficients is adequate to describe a given interspecific interaction depends on the mechanism of the interaction. There are presently two published models of which I am aware that result in constant competition coefficients. One is based on an exploitative mechanism of competition (MacArthur 1968, 1972), and the other is based on interference competition (Schoener 1973). These models are reviewed here. I suggest that (1) they are based on several assumptions which are seldom satisfied, and (2) more reasonable assumptions lead to nonconstant competition coefficients.

The only model of exploitative competition which incorporates the mechanism of competition explicitly and leads to constant competition coefficients is one proposed by MacArthur (1968). The model was further developed by MacArthur (1970, 1972) and Schoener (1974), and has been used in theoretical studies by Lawlor and Maynard Smith (1976) and Holt (1977). The basic assumptions of the model are as follows: (1) Two or more consumer species compete for a number of resources, all of which renew according to the logistic equation. (2) The consumers have linear functional responses; i.e., the amount of resources consumed by an individual per unit time is a linear function of resource densities. (3) Consumer population per capita growth rates are linear functions of the amount of resources consumed. (4) Each consumer and resource population is assumed to be homogeneous, so there is no genetic or size/age specific variation in resource utilization. (5) Population processes in the resource populations occur at rates that are much faster than the consumer population processes. (This last assumption is not explicit in MacArthur's presentation.) (6) No resource populations are driven to extinction by their consumers. (7) There is no lag in the consumer's population response to resource densities. (8) Resources do not interact with each other.

If all of the above assumptions are satisfied most of the time, for most natural communities, then one would expect competition coefficients to be constant. Constant competition coefficients would also be expected if most alternative assumptions also resulted in constant competition coefficients. I will therefore try to show for most of the above assumptions that (1) the assumption is seldom satisfied, and (2) alternative assumptions result in nonconstant competition coefficients. This is not true in every case: I note below that assumption (3) is not critical to producing a model with constant competition coefficients.

The assumption that resource population processes occur at a fast rate relative to consumer population processes (assumption 5) allows one to solve the resource differential equations for steady-state resource densities  $\hat{R}_k$ . The per capita resource consumption of species  $i$ ,  $Q_i$ , is then the sum of the products of consumption rates per unit resource multiplied by steady-state resource densities.

$$Q_i = \sum_k C_{ik} \hat{R}_k. \quad (1)$$

In MacArthur's model, the consumption rates per unit resource,  $C_{ik}$ , are constant. However, they can be functions of resource densities. The steady-state resource abundances are functions of consumer densities. The per capita rate of increase of species  $i$  is then some function of  $Q_i$ , say  $g_i(Q_i)$ . If competition is not purely exploitative, the per capita rate of increase may be a function of the population densities of consumers, independent of  $Q_i$ . Assuming competition is exploitative, the statement that the competition coefficient is constant is equivalent to the statement that

$$\left( \frac{\partial g_i}{\partial N_j} \right) / \left( \frac{\partial g_i}{\partial N_i} \right)$$

is a constant (by definition). This statement can be simplified as follows:

$$\alpha_{ij} = \frac{\partial g_i}{\partial N_j} / \frac{\partial g_i}{\partial N_i} = \left( \frac{\partial g_i}{\partial Q_i} \cdot \frac{\partial Q_i}{\partial N_j} \right) / \left( \frac{\partial g_i}{\partial Q_i} \cdot \frac{\partial Q_i}{\partial N_i} \right) = \frac{\partial Q_i}{\partial N_j} / \frac{\partial Q_i}{\partial N_i}. \quad (2)$$

This shows that MacArthur's assumption that the  $g_i$  are linear functions of resources consumed is not essential for deriving constant competition coefficients, since  $\alpha_{ij}$  does not depend on  $g_i$ . The form of the competition coefficient is sensitive to the remaining assumptions, however.

First, consider the assumed logistic renewal of resources. This assumption may be relaxed by postulating that resources grow according to the following equation which has been proposed by Gilpin et al. (1976):

$$\frac{dR_i}{dt} = r_i R_i \left[ 1 - \left( \frac{R_i}{K} \right)^\theta \right]. \quad (3)$$

Logistic growth is a special case of this model which assumes  $\theta = 1$ . This equation can be solved for the steady-state resource density and competition coefficients may be derived as outlined above. The resulting expression for the competition coefficient of species  $\ell$  on species  $k$  is

$$\alpha_{k\ell} = \frac{\sum_i c_{ik} K_i \frac{1}{\theta} \left( 1 - \frac{1}{r_i} \sum_j c_{ij} N_j \right)^{\left( \frac{1}{\theta} - 1 \right)} \frac{c_{i\ell}}{r_i}}{\sum_i c_{ik} K_i \frac{1}{\theta} \left( 1 - \frac{1}{r_i} \sum_j c_{ij} N_j \right)^{\left( \frac{1}{\theta} - 1 \right)} \frac{c_{ik}}{r_i}}. \quad (4)$$

There are only two cases for which this is not a function of population densities: (1) when  $\theta = 1$  so resource growth is logistic, and (2) when  $c_{ij}$  is the same for all  $i$  and  $j$ . This second condition means that all consumer species have identical resource utilization patterns, a situation which has never been documented for a natural community. Several other plausible resource renewal functions give similar results to equation (3). Thus, it appears that logistic renewal of resources is required to derive constant competition coefficients. As I have pointed out elsewhere (Abrams 1975), Schoener's (1973) summary of data on single species population growth suggests that logistic growth is relatively uncommon in animal communities. Harper (1977) reaches a similar conclusion after reviewing studies on plant population growth. This information alone would be sufficient to suggest that constant competition coefficients are unlikely.

The second assumption listed above is that consumption rates per unit resource are constants; i.e., that the functional responses of resource consumers to resource densities are linear. I have shown elsewhere that nonlinear functional responses result in competition coefficients that are functions of the population densities of consumers (Abrams 1980). Although there is little data on functional responses in the field, most laboratory studies show that animals have nonlinear functional responses (Murdoch and Oaten 1975). Thus, the fact that the competition coefficients in MacArthur's model are constant depends on the further unlikely assumption that all functional responses are linear.

MacArthur's model differs from most natural systems in its assumption that populations are uniform and that they consume resources in a uniform environment. There are many possible ways of introducing nonuniformity into either the consumer populations or the environment. If different size or age classes differ in their resource utilization, then the relative amounts of competition between dif-

ferent size classes will differ. The overall competition coefficient will be constant only if the proportions of each species in each size or age class do not change as overall population density changes. Most factors which affect populations (e.g., predators, physical extremes) are unlikely to affect each size class equally. As a result, competition coefficients will not be constant. Similarly, if there are different habitats and the relative amounts of inter- and intraspecific competition are different in each habitat, then competition coefficients will only be constant when the proportion of each species in each habitat remains constant as population densities change. It seems likely that species will concentrate in the most attractive habitats when population densities are low, leading to a change in the competition coefficients.

Even if MacArthur's model is applicable, competition coefficients will change whenever a resource is driven to extinction (assumption 6 is not satisfied). As Holt (1977) has shown, extinction of at least one resource is likely as the number of resources which are consumed increases.

Both MacArthur's and the present analysis have assumed that the consumer-resource system has a stable equilibrium point. This is not necessarily true. Limit cycles of population densities may arise as the result of either time lags in consumer response to resource density or relatively slow resource population dynamics coupled with certain kinds of functional responses. In either case, consumer and resource population densities will be constantly changing. Because competition coefficients generally depend on the relative densities of different resource types, the competition coefficient is likely to change during the course of a population cycle.

Most sorts of interaction between resources (assumption 8) will lead to non-constant competition coefficients unless the interaction between resources is itself linear. If resources compete with each other, then (given all of the other assumptions of MacArthur's model) competition coefficients between consumer species will only be constant if the competition coefficients between resources are themselves constant. This is unlikely for the same reasons that competition coefficients between consumers are unlikely to be constant. Traditionally, studies of competing consumers have not looked for interactions between resources, so it is not known how often they occur.

In the above discussion I have considered alternatives to assumptions 1-8, individually. It might be argued that if several assumptions were violated simultaneously different factors might cancel, leading to constant competition coefficients. Although it is impossible to exclude the possibility that this could happen in some cases, it would require extremely improbable balancing of parameters in the alternative assumptions considered here. Thus, the conclusion of the entire analysis is that linear competitive effects are very improbable if competition is exploitative.

Interference competition can occur when one organism harms another directly (as in agonistic encounters) or when an organism excludes others from access to a share of resources (as in territoriality). In the former case, constant competition coefficients could result if organisms encountered each other at random, and the intensity of agonistic encounters did not change as a function of population

densities. This is the basis of a model which was proposed by Schoener (1973). As he noted, this model requires that an animal be able to enter into new behavioral interactions while it is engaged in an interaction. Alternatively, it requires that the proportion of time spent in interactions be a very small part of the total activity time. In addition, to obtain constant competition coefficients, one must assume that the propensity of an animal to enter into an agonistic interaction and the intensity of the interaction be unaffected by the number of interactions. I know of no data showing this to be the case for any species of animal. No such data were presented in Schoener's (1973) paper. In contrast, there are a number of studies which have shown that intensity of interactions or the probability of engaging in an agonistic interaction are functions of population density (see Hinde 1970, p. 343; Southwick 1970, pp. 1-13). Interference competition may be expected to evolve as a response to exploitative competition (Case and Gilpin 1974), and the interaction of exploitation and interference is another possible source of nonlinear competitive effects. Several studies (Albrecht 1966; Hazlett 1966) have shown that hunger increases aggressive behavior. Even if the exploitative competition were linear, this interaction of hunger and aggression would result in the overall interaction being nonlinear.

Interference in the form of exclusion from access to resources, by its very nature, should produce nonconstant competition coefficients. If there is an upper limit to territory size, then there will be very little competition (competition coefficients near zero) until the community is filled by individuals possessing maximum-sized territories. Afterwards, territories will be compressed or individuals without territories will be relegated to suboptimal habitats, resulting in much larger competition coefficients. Thus, it appears that realistic models of interference competition will not result in constant competition coefficients either.

Given the available deductive arguments suggesting that constant competition coefficients are not likely to be observed, it would seem relatively unprofitable to continue studies which attempt to determine whether these parameters are in fact constant in specific communities. A more profitable approach would be to try to determine the mechanism of the competitive interaction in as quantitative a fashion as possible. This would normally allow one to deduce how close to constant competition coefficients are, and would provide some biologically useful information as well.

It is difficult to rule out the possibility of someone thinking of a widely applicable model that would lead to constant competition coefficients. However, the paucity of previously proposed mechanisms that would generate constant competition coefficients in spite of the Lotka-Volterra model's preeminent position in animal population biology over the last 50 yr suggests that this is unlikely.

Finally, it should be stressed that neither this note, nor the empirical studies of Smith-Gill and Gill (1978 and other references listed therein) justifies the conclusion that "linear approximations of competition coefficients are probably insufficient and misleading" (Smith-Gill and Gill 1978, p. 568). Even when competition coefficients change as a function of population densities, the assumption of constancy may be sufficient if one is concerned with phenomena in a restricted range of population densities. The size of this range will depend both on the degree

of accuracy desired and on how rapidly the competition coefficients change with population densities. If future research focuses on the mechanisms of competitive interactions, it should be possible to predict the extent and nature of the change in the competition coefficients with population density.

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