PUTTING THE PIECES TOGETHER: TESTING THE INDEPENDENCE OF INTERACTIONS AMONG ORGANISMS

J. TIMOTHY WOOTTON
Department of Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. An important challenge in ecology is determining the degree to which the dynamics at one level of organization can be predicted by the behavior of its component parts at a lower level of organization. This endeavor is likely to succeed only if the behavior of the component parts remains essentially the same regardless of the state of other elements in the system. For example, the behavior of multi-species communities is predictable from a knowledge of interactions among species pairs only if the functions describing the pairwise interactions are not modified by the abundance of other species in the community. Here I discuss some of the problems in identifying empirically whether such interaction modifications ("higher order interactions") occur. Four persistent problems include (1) confusion about the definition of "higher order interactions," (2) discrepancies between the currency typically used in theoretical work (instantaneous rates) and that required in empirical work (the states of variables [e.g., abundances] after a discrete time period), (3) frequent incongruities between statistical procedures and the underlying theory being tested, and (4) a failure to explicitly consider the theoretical framework being tested. Progress may be more rapid in the future if the theory being tested is specified, and if empirical investigations shift their focus toward identifying possible mechanisms by which interactions can be modified.

Key words: difference equations; differential equations; higher order interactions; indirect effect; interaction modification; species interactions.

INTRODUCTION

Like most scientists, ecologists usually take a reductionist approach that attempts to develop some mechanistic understanding of a system by studying the workings of its component parts. For example, studies may examine how different factors influence reproduction, mortality, and dispersal patterns to obtain more precise predictions of the dynamics of populations, or they may investigate how populations of particular species interact to predict the dynamics of multi-species assemblages. Regardless of the level of investigation, the discoveries of reductionist studies ultimately must be pieced together in order to predict the workings of the entire system. For this endeavor to be successful, the behavior of the component parts must remain essentially the same regardless of the state of the other parts of the system. Whether component parts interact independently of one another remains an open question at all levels of ecology.

This question has perhaps received the most attention in the study of multi-species communities under the term "higher order interactions" (HOI). For several decades, community ecologists have considered whether simple equations describing the interactions between species pairs (or other environmental variables) independent of other species can be combined to model successfully the dynamics of multi-species communities (Vandermeer 1969, Wilbur 1972, Neill 1974, Menge 1978, Case and Bender 1981, Pomerantz 1981, Abrams 1983, Miller and Kerfoot 1987, Morin et al. 1988, Van Buskirk 1988, Fauth 1990, Wilbur and Fauth 1990, Strauss 1991, Worthen and Moore 1991, Wootton 1992, 1993). If the interaction between two species is modified by other species, new higher order terms are required to successfully model a system, often making the model harder to analyze and parameterize.

Despite this long history, there still appears to be considerable confusion in the literature regarding what HOI really are, and how they should be investigated. Focusing on a mechanistic definition (modifying an interaction, Wootton 1993) rather than a mathematical

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1 For reprints of this Special Feature, see footnote 1, page 1527.
2 Present address: Department of Ecology and Evolution, 1101 East 57th Street, University of Chicago, Chicago, Illinois 60637-1573 USA.
criterion (higher order interaction) may aid field investigations that examine whether pair-wise interactions can be combined to capture the dynamics of multi-species communities. In some settings, finding higher order relationships may simply mean that species pairs interact in a nonlinear manner (Case and Bender 1981, Pomerantz 1981); clearly the fact that interactions between species pairs are not linear does not prevent ecologists from combining descriptions of interactions between species successfully. Mechanistically, HOI attain importance only if they arise because a change in the abundance of a third species alters the function describing the per capita interaction between two other species (Abrams 1983, Miller and Kerfoot 1987, Wooton 1993). For example, macrophytes might affect the ability of fish to find zooplankton prey through visual interference (Crowder and Cooper 1982). This mechanistic outlook also serves to emphasize that finding indirect effects of one species on another does not necessarily mean that the behavior of multi-species systems cannot be predicted by knowing the interactions between species pairs. Many indirect effects arise as a consequence of chains of direct interactions, not by modifying how other species pairs interact. If field observations of interactions among species can be mechanistically described in terms of one species modifying how two other species (or individuals within a species) interact (e.g., crypsis), then this interaction can be identified a priori as requiring some sort of higher order term in a model.

Although it is straightforward to develop mechanistic hypotheses for how an interaction modification might arise, it is difficult to examine standard population-level data and determine whether they indicate such "higher order" interactions. The standard approach has been to focus initially on whether the dynamics of multi-species systems deviate from those predicted by the simplest models, such as those in which species additively affect the growth rates of other species (Vandermer 1969, Neil 1974, Gilpin et al. 1986). Unfortunately, complications can arise when testing even the simplest models because the type of model that is most tractable theoretically is not necessarily most tractable experimentally. In this paper, I highlight some of these complications and discuss their implications. Specifically, I point out that examinations of statistical interactions only have meaning when they can be tied directly to a particular model of community interactions. Furthermore, properly testing for interaction modifications is complicated by the fact that whereas theoretical models focus upon instantaneous population growth rates as the variables of interest, experimentalists typically observe populations at discrete points in time and can only recover instantaneous growth rates after making very specific assumptions.

**What Model Is Being Tested?**

**Differential vs. discrete-time equations**

Theoretical developments of models of multi-species communities generally use differential equations (MacArthur and Levins 1967, May 1973, Levine 1976, Adler and Morris 1994). Differential equations are often easy to analyze, and are most appropriate to situations where approximately instantaneous rates of change can be measured (e.g., rates are constant over the time interval studied). A general representation of differential equations standard to community ecology theory is

$$dN_i/dt = N_i \sum_{j=1}^{m} f_j(N_i)$$

where $N_i$ is the abundance of the $i$th species in an $m$-species system, and $f_j(N_i)$ is the function describing how the abundance of species $j$ affects the growth rate of species $i$.

Based on this general differential equation, Case and Bender (1981) presented a method to test whether interactions between species pairs were independent of species composition. Their approach is especially useful because it does not require particular functional relationships (e.g., linear or nonlinear) between species pairs to be specified beforehand, nor does it require a particular form of any interaction modification to be specified. For example, Case and Bender (1981) showed that in a system with three species ($A$, $B$, and $C$) at initial densities $a$, $b$, and $c$, pair-wise interactions would be sufficient to model the system if one independently manipulated each species (to densities $a'$, $b'$, and $c'$) and found that:

$$\frac{1}{a} \frac{dA}{dt} (a, b, c) + \frac{1}{b} \frac{dB}{dt} (a, b, c) + \frac{1}{c} \frac{dC}{dt} (a, b, c)$$

where $dA/dt$ is the instantaneous growth rate of species $A$. As Morin et al. (1988) and Wilbur and Fauth (1990) point out, this is exactly how interaction terms are tested in an analysis of variance. It is important to emphasize, however, that this test deals with per capita population growth rates. Unfortunately, instantaneous
population growth rates are difficult to measure directly; empirical studies more naturally measure variables such as abundance, biomass, and elapsed time. Of course, population growth rates can be estimated from censuses of abundance or biomass if one is willing to assume a particular underlying functional form.

Although theoreticians usually choose to work with differential equations, empiricists cannot conduct experimental tests over an instantaneous time scale. Consequently, the experimental perspective favors asking questions about interaction modifications in terms of discrete-time models, which deal directly with measurable quantities such as abundance or biomass. Unfortunately, there is no one-to-one correspondence between difference equations and differential equations (Van der Vaart 1973), yet proper statistical tests depend on which form is chosen. For example, one analogous difference equation model for an $m$-species community adds together the effects of other species (May 1973), and hence takes a form similar to Eq. 1:

$$N_{i,T + t} = N_{i,T} \sum_{j=1}^{m} f_{ij}(N_{i,T})t,$$

where $N_{i,T}$ is the abundance of species $i$ at initial time $T$, and $t$ is the elapsed time between censuses (usually scaled so that $t = 1$). Once a difference equation analog of Eq. 1 has been chosen, one can use it to identify the proper transformation to estimate population growth rates and then apply the Case and Bender (1981) method to these rates. If Eq. 2 is assumed, one need only divide by $t$. Alternatively, one can identify the appropriate statistical comparison to analyze the measurements (e.g., abundances) taken directly from the different treatments. For example, if the form of Eq. 2 is assumed, one can compare directly population densities or biomass in the same manner that the Case and Bender (1981) method compares per capita population growth rates among treatments, since Eq. 2 assumes that the effects of different species on densities are added together. In general, studies testing for interactions using ANOVA on untransformed density data are implicitly assuming that Eq. 2 is the underlying model for community dynamics.

A more popular difference equation is a Ricker-type equation (e.g., Van der Vaart 1973, Comins and Hassell 1976, Hassell and Comins 1976, Hofbauer et al. 1987), which takes the form

$$N_{i,T + t} = N_{i,T} e^{\sum_{j=1}^{m} f_{ij}(N_{i,T})t},$$

where $N_{i,T}$ is the abundance of species $i$ at time $T$, $e$ is the base of the natural log, $f_{ij}(N_{i,T})$ is the function describing the effect of the $j$th species on species $i$, and $t$ is the elapsed time from initial conditions (again, the equation is usually scaled so that $t = 1$).

Again, a method to compare abundances directly can be derived assuming that Eq. 3 describes the underlying form of community dynamics. Eq. 3 implies that over discrete time, the effects of variables on population size are combined in a multiplicative manner, rather than the additive manner in Eq. 2. Therefore, testing whether the dynamics of the community modeled under the assumption that interactions are independent of other variables requires a multiplicative test of abundances. Consider a three-species version of the general system given by Eq. 3, where the three species are $A$, $B$, and $C$, and we ask whether the effects of $B$ and $C$ on $A$ are independent of one another. We first write the difference equations for $N_{A,T+1}$ in terms of control levels of $A$, $B$, and $C$ ($N_{A,T}$, $N_{B,T}$, and $N_{C,T}$, respectively) and experimental levels of species $B$ and $C$ ($N_{B,T}$ and $N_{C,T}$, respectively) as:

$$N_{A,T+1}(N_{A}, N_{B}, N_{C}) = N_{A,T} e^{f_{i1}(N_{A,T})} e^{f_{i2}(N_{B,T})} e^{f_{i3}(N_{C,T})},$$  

$$N_{A,T+1}(N_{A}, N_{B}, N_{C}) = N_{A,T} e^{f_{i1}(N_{A,T})} e^{f_{i2}(N_{B,T})} e^{f_{i3}(N_{C,T})},$$

$$N_{A,T+1}(N_{A}, N_{B}, N_{C}) = N_{A,T} e^{f_{i1}(N_{A,T})} e^{f_{i2}(N_{B,T})} e^{f_{i3}(N_{C,T})},$$

$$N_{A,T+1}(N_{A}, N_{B}, N_{C}) = N_{A,T} e^{f_{i1}(N_{A,T})} e^{f_{i2}(N_{B,T})} e^{f_{i3}(N_{C,T})}.$$  

Therefore, if the effects of $B$ and $C$ on $A$ are independent of each other, one should find that:

$$N_{A,T+1}(N_{A}, N_{B}, N_{C}) N_{A,T+1}(N_{A}, N_{B}, N_{C}) = N_{A,T+1}(N_{A}, N_{B}, N_{C}) N_{A,T+1}(N_{A}, N_{B}, N_{C}).$$

This multiplicative hypothesis can be tested statistically in a number of ways, including contingency table analysis (such as log-linear tests and their relatives), or tests that directly compare the appropriate products of observed densities in different treatments (see Wootton 1992, 1993). Alternatively, because Eq. 3 is a discrete time analog of Eq. 1, the Case and Bender (1981) method can be applied by using ANOVA and related methods after estimating population growth rates with a multiplicative (i.e., log) transformation of density data (Sokal and Rohlf 1981, see Case and Bender 1981, Wilbur and Fauth 1990).

In summary, when one writes an explicit model of
species interactions, there is no ambiguity about what would comprise an interaction modification or higher order interaction. However, when one applies statistical approaches such as ANOVA to experimental data, distinctions between additive and multiplicative statistical models are important because these distinctions correspond to different hypothesized underlying models.

*Implications for empirical studies*

Although the goal of the two simple difference equation formulations represented by Eqs. 2 and 3 are similar and both can be translated into a differential equation model of the form given by Eq. 1, the details of each model make a huge difference with respect to testing for interaction modifications. For example, most experiments testing for interactions in the effects of variables are analyzed with ANOVA, which assumes, among other things, normal distributions and homogeneous variances. In order to meet these assumptions, data are often log-transformed. Investigators should be aware that choosing whether or not to use a transformation also inherently affects the underlying assumption of which form of model is being tested in a given community. Therefore in some cases, attempts to best meet statistical assumptions may conflict with proper testing of the most appropriate model for the situation under study.

Second, testing difference equation analogs of differential equations dictates that certain experimental designs be used. Specifically, because the predictions of the equations are functions of fixed densities of other species ($N_j$ in Eqs. 2 and 3), proper experimental tests require that the densities of manipulated species be held constant. When species composition is changed but the densities of the manipulated species are allowed to vary freely, interactions detected by statistical analysis may be caused by chains of direct interactions, rather than the result of interaction modifications. Because discrete-time models best match experimental situations, testing for interactions among treatments that are not fixed does not necessarily tell us whether the dynamics of communities can be captured on the basis of knowing how species pairs interact. One attempt to solve the problem created by densities of manipulated variables changing during the course of the experiment might be to use an analysis of covariance. This will not, however, be straightforward, since changes in the densities of experimentally manipulated species under such circumstances will usually be some complex integral of the densities of all species, rather than a simple linear relationship between species pairs.

Third, it is important to state which difference equation model is being assumed in various empirical settings, and ask whether one form tends to describe ecological systems better. When do conclusions derived by assuming an additive difference equation model differ radically from those of a multiplicative difference equation model in empirical studies? The most obvious example can be illustrated for the system of three species described by Eqs. 4a–d and 5. Suppose that species $A$ starts out with equal numbers of individuals in each of four treatments ($A$ alone, $A$ and $B$ together, $A$ and $C$ together, all three species together), and that in the absence of species $B$ and $C$, the population of species $A$ numbers 100 at the end of the experiment. Suppose further that species $A$ numbers 40 in the presence of $B$ alone, and 30 in the presence of $C$ alone. An additive difference equation without an interaction between $B$ and $C$ predicts that the population of $A$ when all three species are together should be $-30$, clearly an impossibility? Therefore an additive statistical test on population abundance will naturally be biased towards finding a positive interaction between $B$ and $C$.

In contrast, a multiplicative model predicts that $A$ should have a population size of 12 when all three species are together, thus positive, negative, and zero interactions among variables are all possible outcomes of the data.

*An empirical evaluation of additive vs. multiplicative statistical models*

Because most empirical studies of interactions between variables have been analyzed with additive models of population density, it is worth considering the consequences (using published examples) of using multiplicative tests of interactions among species or other environmental variables instead. I examined 18 studies (Table 1) that all considered whether variables interacted with each other, and that represented a range of ecological systems (marine, freshwater, terrestrial). All report experiments that manipulate at least two species (or other environmental variables) in a factorial design to test for interactions among variables. For ease of presentation, I consider only two-way interactions in this summary. Four studies utilized multiplicative statistical tests or transformations to avoid the problems described above (Case and Bender 1981, Wilbur and Fauth 1990, Wootton 1992, 1993). A fifth study tested for interactions with both multiplicative and additive models (Fowler and Rausher 1985). Two other studies (Van Buskirk 1988, Martin et al. 1989) recognized the difficulties of additive models when they compared observed survivorships to those expected in a multiplicative model to estimate the magnitude of interaction effects, yet they used additive models to test statistically for interactions among variables. One study approximated a multiplicative test by taking the $e^{-t}$ root of the data, where $t$ was the elapsed time in days (Morris 1992). One study analyzed square-root
TABLE 1. Summary of comparisons between predictions of additive and multiplicative discrete-time equations in published empirical studies examining interactions among manipulated variables.

<table>
<thead>
<tr>
<th>Study</th>
<th>Test type*</th>
<th>Number of tests</th>
<th>Additive prediction impossible†</th>
<th>Additive fits better‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilbur (1972)</td>
<td>add.</td>
<td>11</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Case and Bender (1981)</td>
<td>mult.</td>
<td>6</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Crowder and Cooper (1982)</td>
<td>none</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Wilzbach et al. (1986)</td>
<td>none</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Fowler and Raisher (1985)</td>
<td>both</td>
<td>3</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Wilbur (1987)</td>
<td>add.</td>
<td>15</td>
<td>13</td>
<td>3</td>
</tr>
<tr>
<td>Morin et al. (1988)</td>
<td>add.</td>
<td>3</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Van Buskirk (1988)</td>
<td>add.</td>
<td>4</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Martin et al. (1989)</td>
<td>add.</td>
<td>10</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>Fauth (1990)</td>
<td>add.</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Huang and Sih (1990)</td>
<td>add.</td>
<td>5</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Hurd and Eisenberg (1990)</td>
<td>add.</td>
<td>18</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Wilbur and Fauth (1990)</td>
<td>mult.</td>
<td>3</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Fauth and Resetarits (1991)</td>
<td>add.</td>
<td>5</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Worthington and Moore (1991)</td>
<td>sqrt.</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wootton (1992)</td>
<td>mult.</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Morris (1992)</td>
<td>t-root</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wootton (1993)</td>
<td>mult.</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>94</td>
<td>53</td>
<td>9</td>
</tr>
</tbody>
</table>

* Type of statistical test or transformation used in the paper; add. = additive, mult. = multiplicative, sqrt. = square-root transformation, t-root = t^n root transformation, both = both additive and multiplicative, none = no test done.
† Number of instances where additive tests predicted impossible (negative) population sizes.
‡ Number of comparisons where the predictions of additive models better fitted the data (abundances, total biomass, or survivorship) than did multiplicative models. Models fit equally well in three cases.

transformed data (Worthington and Moore 1991), which does not correspond to the structure of either model. Two studies (Crowder and Cooper 1982, Wilzbach et al. 1986) did not present tests for the specific interactions in the manipulated variables. The bulk of the studies (seven) used additive models.

When comparing the predictions of difference equations, several patterns indicate that multiplicative statistical models are usually most appropriate to apply to experimental data on abundance, biomass, or some related measure (e.g., survivorship). First, as a whole, observed mean values of variables most closely matched expected mean values from multiplicative models (81/94 cases) far more frequently than those from additive models (9/94 cases, Table 1). This result does not mean necessarily that multiplicative models give an adequate fit to all 81 cases. Indeed, several studies testing multiplicative models have found the data to deviate significantly from expectations (Case and Bender 1981, Fowler and Rausher 1985, Wilbur and Fauth 1990, Wootton 1992). Second, in 53 of 94 cases (56%), additive difference equations predict impossible (negative) expected mean population sizes (Table 1); multiplicative difference equations never predict impossible values. Therefore, in many cases additive models are clearly inappropriate. Third, most populations that have been observed at relatively low density grow multiplicatively (exponentially) over time (Gause 1934, Elton 1958, Wootton 1987), not additively (linearly). Fourth, investigating the effects of different factors on a particular species can usually be phrased in terms of survivorship probabilities relative to the treatment in which the species performs best. Combining probabilities of survivorship is usually done multiplicatively (Wilbur and Fauth 1990, Wootton 1992, 1993).

The analysis also showed that differences in expected values for additive and multiplicative models differ little when the magnitudes of the effects of variables in isolation are relatively small over the time period studied (e.g., Huang and Sih 1990). This agrees with the convergence of additive and multiplicative difference equations to the differential equation over short elapsed times, and suggests the biases in using an additive test of density might be reduced by collecting data over a short period of time. This strategy has two limitations from a practical standpoint. First, because of the logistical difficulties in conducting numerous, adequately replicated experiments, it is desirable to use efficient experimental designs that address multiple questions simultaneously. For example, in factorial experiments, one is usually interested in the importance of each manipulated variable in isolation as well as the degree to which the variables interact. Reducing the experimental time period tends to reduce the magnitude of differences between all treatments, hence reducing the investigator's power to detect individual treatment effects against a background of environmental variation and sampling error. Second, many models, including those of Eq. 1, assume that the per capita effects of interactions under a given set of conditions
are constant through time. In reality, they may vary because of changes in activity levels (e.g., changes with diel or tidal cycles) or because the interaction is not spatially homogeneous relative to the scale feasible for experimentation or sampling. For example, in experiments manipulating the access of bird predators to plots in an intertidal community (Wootton 1993), birds may not be present at a particular experimental site at a specific point in time, but they will visit the site at some time during an experiment of adequate duration. Over substantially shorter time periods, the ability to estimate the average effect of a factor for each replicate would be compromised. Because of these limitations, testing a multiplicative discrete-time model may be a more desirable alternative to shortening the experiment to allow the application of an additive test when testing models taking the general form of Eq 1.

Although models of community dynamics are concerned with changes in population density or biomass, analyses in terms of effects on individual body sizes may provide insight because body size often determines survival probabilities and fecundities. The effects of variables on body size often may be best considered in a multiplicative context for several reasons. Usually observed trajectories of body size over time are better approximated with an exponential model rather than a linear model, so differences in growth rate among treatments should change multiplicatively over time (e.g., Wilbur and Collins 1973). Furthermore, the effects of body size on population size are often multiplicative rather than additive. Within a species, increases in body size usually increase fecundity in a nonlinear manner (e.g., Spight and Emlen 1976, Kaplan and Salthe 1979, Peterson 1986) and reduce the age at first reproduction (Smith 1987, Semlitsch et al. 1988), which multiplicatively affects population growth rate. Clearly, underlying models of individual growth and its relationship to population dynamics also must be considered in order to determine what type of statistical test is appropriate for such measures of individual performance.

**Future Directions**

Determining the ability of models describing interactions at the population level to predict patterns of multi-species assemblages remains a central problem in ecology. Three general areas of investigation seem most important for future work. First, posing the problem around a mechanistic definition (interaction modifications) rather than a mathematical definition (higher order interactions) raises the question of what specific mechanisms might cause one species to change how other species interact. At this time, natural history observations directed at this question are likely to provide the most rapid progress. Our goal should be to efficiently identify aspects of natural systems for which complex interaction terms may have to be included in corresponding models.

A second question, the importance of interaction modifications in natural situations, remains a key area of investigation. At one level, Abrams (1983) has argued that interaction modifications should be quite common, so the question of whether they exist may not be especially interesting. Instead, the major question is how strongly do they affect the dynamics of ecological systems. For example, Morin et al. (1988) discussed what proportion of variance could be attributed to the interactions among manipulated species detected in their analysis and concluded that the effects were relatively weak. Answering this question will demand experiments that are sensitive to the nature of the underlying theory and the difficulties of testing it. The experimental strategy will require the use of statistics that match the theory and applying theory that matches the experimental constraints of the system being studied. For example, one could conduct factorial experiments in which the densities of manipulated species are held constant and use the additive or multiplicative statistical approaches described above to test specific models. Alternatively, focusing on the mechanisms that cause changes in interactions allows a different approach. Any potential interaction modifications that can be identified could be manipulated to unambiguously assess their effects. For example, sessile invertebrates make limpets less susceptible to bird predators in intertidal communities through crypsis (Wootton 1992, 1993). By manipulating the coloration of sessile species to reduce the possible cryptic effect, one could determine directly the importance of crypsis to limpets.

A third important area of research is the development and evaluation of alternative functional forms to Eq. 1 that may better describe our mechanistic understanding of particular processes (Fowler and Rauscher 1987, Adler and Morris 1994). For example, competition for light might affect population growth rates in a multiplicative rather than an additive manner if each plant captures a fraction (rather than a given amount) of the light it encounters (Adler and Morris 1994). Such approaches might also include features (e.g., body size, defensive ability) that are at the root of some higher order interactions. It will be critical to determine appropriate statistical tests and experimental designs that apply to these models.

**General Conclusions**

I have illustrated several issues involved in testing whether the effects of different variables on a target variable are independent of one another. Although my discussion has focused on biotic interactions in multi-
species communities, the issues I raise apply to studies ranging from autecological to ecosystem perspectives and including both abiotic and biotic factors. For example, one of the most basic aspects of predator behavior is the predator's functional response. Key to studies of functional responses is an examination of whether or not predators interfere with one another. Statistically this issue translates into a test of whether or not there is an interaction between predators with respect to effects on consumption rates. If the per capita number of prey consumed declines with increasing predator density, interference among predators is often identified as the cause (i.e., additional predators modify the ability of a single predator to feed). Because experiments are conducted over discrete time, however, such a declining pattern is expected without interference. The probability of a prey individual not being eaten by any of \( N \) predators is equal to the probability of not being eaten by a single predator raised to the \( N \)th power, so the number of prey consumed is not expected to increase linearly with predator density (Fig. 1).

Testing whether interactions among organisms are independent of species composition is an important area of active research, but proper tests require more than examining interaction terms in a factorial ANOVA. One must specify what underlying model is being assumed, and the failure of one model structure does not necessarily mean that no other model will be successful (see Adler and Morris 1994). This fact highlights the importance of identifying the mechanisms that act to modify an interaction in a given situation. When such mechanisms are identified, the failure of a simple model to capture community dynamics can be attributed to an interaction modification with more confidence. Finally, the structure of models assumed to underlie community dynamics can have profound consequences for tests of independence in interactions. Exploration of higher order effects is not as simple as asking whether significant interactions are evident in a factorial ANOVA experiment.

**ACKNOWLEDGMENTS**

This paper was stimulated by discussions and correspondence with F. Adler, T. Case, P. Kareiva, L. Goldwasser, P. Morin, W. Morris, C. Osenberg, M. Power, and W. Sousa. The Miller Institute for Basic Research at U.C. Berkeley and N.S.F. grants BSR-91-00123 and BSR-91-06881 provided financial support.

**LITERATURE CITED**


