

## Competition and the Form of Habitat Shift

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This study derives simple models of competition and applies them to the description and prediction of habitat shift. *Habitat shift* is a change from one species population to another in the habitats occupied by most of their individuals.

*Interference* models in which individuals are limited in their time for feeding by other individuals can give rise to competition equations structurally identical to Lotka-Volterra models. These models have linear zero-isoclines. Interference models in which individuals as a group are energy-limited produce nonlinear, concave downward, zero-isoclines. These are asymptotic to the axes. Unlike the linear-isocline case, such models always produce a unique stable equilibrium. Asymptotes may be made nonzero by inclusion of a refugium into the isocline equation.

*Exploitation* models in which individuals of different species feed with fine-grained selection on the same resources but gain different energies from these give parallel linear isoclines. They cannot produce a stable point equilibrium, whether consumption per individual is fixed or not. A simple model, in which individuals have flexible requirements and feed with fine-grained selection, has a unique stable equilibrium if each species has some resources not usable by the other. This model has concave downward isoclines. If one species utilizes only resource kinds included within those of another, both can coexist if the first is sufficiently better at obtaining the shared resources and if there are enough such resources.

Systems of equations specifying growth of both consumers and resources can sometimes give isoclines that are linear (MacArthur, R. H. 1968, *The theory of the niche in "Population Biology and Evolution,"* Syracuse Univ. Press) or that are of the same curvilinear form as isoclines for the pure consumer systems.

One way to relate competition to habitat shift is to assume the isocline equations hold separately for each of a set of habitats. Then if estimates of carrying capacities are available, models for isoclines can be constructed and competition parameters computed by regression techniques, using data for each habitat as a separate point. Relative carrying capacity in Locality *S* (with competitors) can be estimated as follows. Measure the relative abundance of the species in its "fundamental" niche in Locality *A* (without competitors); then weigh it by the ratio of available resources in Locality *S* to available resources in Locality *A*. This method provides a possible structure for formalizing how competition transforms the "fundamental" into the "realized" niche.

The method is applied to a shift in structural habitat (perch height and diameter) in some Caribbean lizards. Habitat availability is measured as relative

surface area, estimated from vegetation using a new sampling technique. Results are: (1) nonlinear isoclines fit better than linear ones; (2) concave downward isoclines fit much better than convex downward isoclines; (3) an exploitative model fits better than all others, including interference and descriptive models; and (4) competitors of different sizes are more likely to fit interference than exploitative models; those of the same size show the opposite; and species best fitting interference models are more often the smaller member of pairs of differently sized competitors.

## I. INTRODUCTION

Ecologists are often confronted with replicated data on relative occurrences of similar species. These replicates may be more or less isolated units of space, such as habitats, islands or laboratory tanks. It is sometimes interesting to ascertain whether such data indicate negative interactions, such as competition, among the species. The classical model that hypothesizes what abundances of species result from competition is that of Lotka (1932) and Volterra (1926). This model predicts an equilibrium abundance of one species linearly and negatively related to the abundances, possibly nonequilibrium, of cooccurring species. However, abundances can be nonlinearly yet still negatively related. Because the many factors resulting in ecological data often cause it to be highly variable, assuming linearity may even give the wrong qualitative answer to the question of competition when the underlying relation is nonlinear. It therefore might be useful to have a family of models which together cover the relationships to be expected from the major kinds of competition. Such models not only give a more reliable answer to whether competition has occurred, but if certain ones consistently fit certain data, can implicate particular mechanisms.

This study has two major objectives.

The first is to give some assumptions that lead literally or nearly so to Lotka-Volterra models and other assumptions that lead to models with highly nonlinear isoclines but with the same number of free parameters. The purpose is to generate simple models whose isoclines can be conveniently fitted to biological data. Section II develops the models.

The second is to apply the models to a particular example of relative occurrences of species; those species' distributions in units of habitat space. The purpose is to discover the mathematical form and suggest the biological mechanism of habitat shift. Our application of the simple models is not an ideal test for those models. Nonetheless, the coupling does provide a biologically nonarbitrary framework for detecting and measuring competition in nature. Section III describes the application to habitat shift in general terms, and Section IV gives a particular application to extensive data from lizards.

II. MODELS<sup>1</sup>1. *One-level dynamical models*

In order to grow, a population must, after the energy demands of its individuals are met, convert enough energy into offspring to more than replace those members that die. To incorporate this condition into differential-equation models, we may conveniently begin with the following generalized form.

$$dN_1/dt = R_1 N_1 [M_1(N_1, N_2)],$$

where for simplicity we consider only two competing species. Here,  $M$  is the energy per unit time available to a single individual for reproduction beyond replacement.  $R_1$  converts this energy into individuals of Species 1. (This and subsequent terms are explained more fully in Schoener (1973).)  $M_1 = 0$  is the zero-isocline for  $dN_1/dt$ . If the population is to stop growing at some  $N$ ,  $M_1$  must contain at least one term,  $X_1$ , incorporating the energy input per individual and at least one of two cost terms,  $Y_1$  (density-dependent costs) and  $Z_1$  (density-independent costs). All such terms have dimensions: energy/[time  $\times$  number]. We now discuss simple representations of  $X$ ,  $Y$  and  $Z$ .

a. *Input,  $X_i$* 

$X_i$  gives the energy input, after processing of food, that an organism of Species  $i$  has to meet maintenance and activity costs as well as to reproduce. We give three basic forms, each with a different biological interpretation.

i.  *$X_i$  Constant.* Let  $T_i$  be the proportion of the total time an individual spends in feeding and  $\epsilon_i$  be the net energy harvested by an individual feeding for unit time. Then  $E_i = \epsilon_i T_i$  is the net energy harvested per unit activity time.  $E_i$  is limited by (1) the time available for feeding,  $T_i$ , and (2) the effectiveness of feeding,  $\epsilon_i$ .  $T_i$  may be determined by extrinsic circumstances such as the need to perform other activities, but may also be adjusted by the organism to meet a fixed capacity to process food.

ii.  *$X_i$  Linearly Related to Population Size.*  $X_i$  may also be determined by the number and duration of interactions with members of the same or different species. If that number is, as in random collision, proportional to the density of those individuals, then

$$X_1 = E_1 [T_1 - A_{11}(N_1 - 1) - A_{12}N_2] \cong E_1 (T_1 - A_{11}N_1 - A_{12}N_2).$$

Here,  $A_{ij}$  is the time spent by an individual of Species  $i$  in interaction with a single other individual of Species  $j$  per unit time, and  $T$  includes interaction time.

<sup>1</sup> Table of symbols in Appendix 2.

$A$  is inversely proportional to the area or volume in which interactions take place; it represents how interference diminishes the energy available to an animal by cutting into its time for feeding. Frank (1952) has suggested this kind of competitive mechanism in copepods. If exposure time for new interactions is diminished by time spent in interaction, this linear relation is inappropriate (Schoener, 1973), and a quadratic term is more suitable. Hassell (1971) has evidence for nonlinear interference in parasitic insects.

iii.  *$X_i$  Hyperbolically Related to Population Size.* Suppose instead of being time-limited or capacity-limited, organisms were limited by a constant amount of resources collectively available per unit time,  $I$ . Then the share of energy per individual is  $I_{Ei}/N_i$  for resources utilized exclusively by Species  $i$  and  $I_{0i}/(N_i + \beta N_j)$  for resources shared by Species  $i$  and  $j$ . Here  $\beta$  represents the propensity of an individual of  $j$  relative to  $i$  for getting a unit of overlapping resource. Such terms can model the consequences of purely exploitative competition, in which resources are divided among individuals. However,  $\beta$  may not be determined just by such noninteractive characteristics as feeding rate, but also may reflect the animal's investment in interference behavior. For example it may measure the relative territory size of two interspecifically territorial species. Thus while  $\beta$  does not represent interference costs, it can incorporate its results.

b. *Density-Dependent Costs,  $Y_i$*

Making the same assumptions as in a-ii, the energy lost in interaction as well as deaths from interaction should be proportional to density of individuals, e.g.  $Y_i = -\gamma_{ij}N_j$ , where  $\gamma_{ij}$  is the energy cost for an individual of  $i$  in interaction with a single individual of  $j$  per unit time. Where there is risk of death proportional to exposure time, a more complex but still linear term can result (Schoener, 1973).

c. *Density-Independent Costs,  $Z_i$*

$Z_i$  simply represents maintenance or existence metabolism plus whatever density-independent component there is to the death rate.

The three elements of  $M$  can be combined in various ways to give dynamical models of interspecific competition. We now review the simplest such models, whose zero-isoclines are linear or quadratic in the  $(N_1, N_2)$ -plane. Isoclines of higher degree are also possible, but we are guaranteed explicit expressions for only those of first or second degree.

A. *Pure Interference, Input Limited by Feeding Time or Processing Capacity*

To produce equations of Lotka-Volterra form, e.g.

$$dN_i/dt = (r_1N_1/K_1)(K_1 - N_1 - \alpha_{12}N_2), \quad (1)$$

we can combine constant (i) or linear (ii) input terms with cost terms (b) and (c), provided only that at least one such term contains  $N_1$  and  $N_2$ . For example using (a-ii), (b) and (c), we get

$$dN_1/dt = R_1 N_1 [E_1 (1 - \lambda_{11} N_1 - \lambda_{12} N_2) - \gamma_{11} N_1 - \gamma_{12} N_2 - C_1], \quad (2)$$

where  $\lambda_{ij} = A_{ij}/T_i$ . The competition coefficient  $\alpha_{12}$  gives the competitive effect on the population growth of Species 1 by an individual of Species 2 relative to that effect by an individual of Species 1. Equation 2 provides a lower-level translation of this coefficient:  $\alpha_{12} = (\gamma_{12} + E_1 \lambda_{12})/(\gamma_{11} + E_1 \lambda_{11})$ . Isoclines of this model are linear, and its behavior in the  $(N_1, N_2)$ -plane is well known (e.g. Keyfitz, 1970). For two species, if there is an interaction involving positive  $\hat{N}_1$  and  $\hat{N}_2$ , it is either a stable node or a saddle (the "unstable equilibrium" of some texts). For more than two species, conditions for positivity and stability have recently been given by Strobeck (1973).

#### B. Pure Exploitation, Completely Overlapping Resources, Fixed Energy Input to the Populations

Using (a-iii) and (c) we have

$$dN_1/dt = R_1 N_1 [I_{01}/(N_1 + \beta N_2) - C_1]. \quad (3a)$$

The equation for Species 2 is similar except that there is a  $\beta$  in the numerator of  $X_1$ . In (3a)  $K_i = I_{0i}/C_i$ . If we write (3a) as

$$dN_1/dt = ((R_1 V I_{01}) N_1 / K_1) [K_1 - N_1 - \beta N_2], \quad (3b)$$

where  $V = (N_1 + \beta N_2)^{-1}$ , we see that it has trajectories identical to the Lotka-Volterra system (1), since  $dN_1/dN_2$  is structurally the same for both. However, because  $\alpha_{12} = \beta$  and  $\alpha_{21} = 1/\beta$  in (3a), the isoclines are always parallel. This means that the species with the largest carrying capacity will win in competition, so point equilibrium is impossible. Because  $K_i = I_{0i}/C_i$ , the lower the death and maintenance rate and the higher the efficiency of energy extraction for the resource, the greater the chance of winning in competition.

#### C. Pure Interference, Fixed Energy Input to the Populations

For this case, we combine (a-iii) with (b) and (c) to get

$$dN_1/dt = R_1 N_1 [(E_1/N_1) - \gamma_{11} N_1 - \gamma_{12} N_2 - C_1]. \quad (4)$$

Solving  $M_1 = 0$  for the isocline  $\hat{N}_1$ , it is straightforward to show that  $d\hat{N}_1/dN_2 < 0$  and  $d^2\hat{N}_1/dN_2^2 > 0$  throughout. Furthermore, each species'

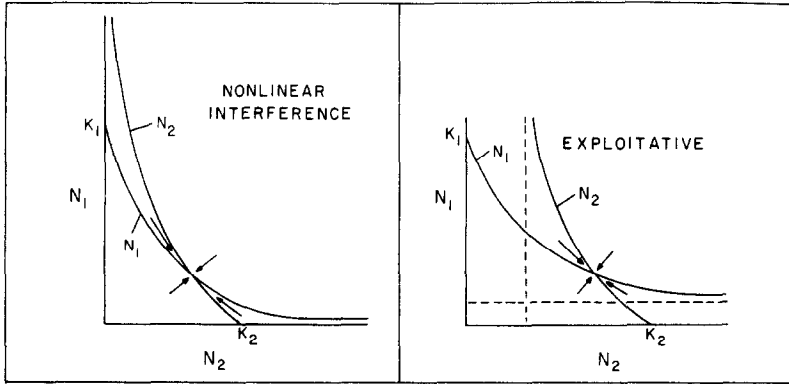


FIG. 1. Two kinds of competition models. Left, Eq. (4); right, Eq. (5).

isocline is asymptotic to the other species' axis. Therefore, the isoclines must intersect at least once in the first quadrant, but it is not obvious from concavity alone how often they intersect. Linearization around equilibrium shows that the eigenvalues are always negative real, so that the singularity is a stable node and the isoclines can intersect only once (Fig. 1). Furthermore, Bendixson's negative criterion, that  $(\partial/\partial N_1)(dN_1/dt) + (\partial/\partial N_2)(dN_2/dt)$  not change sign in the region of interest (Andronov *et al.*, 1966), shows that limit cycles are impossible in the first quadrant. Hence stability is global. These facts imply that Species 1 and 2 must stably coexist and populations approach equilibrium in a nonoscillatory manner.

If there is no intraspecific interference,  $\gamma_{11} = 0$  in Eq. (4). Properties of the resulting model, which is easier to use in the numerical analysis below, are qualitatively identical to (4).

#### D. Pure Exploitation, Resources Partially Overlapping, Fixed Energy Input to the Populations

A second way to model stable coexistence is to add exclusive resources to (3):

$$dN_1/dt = R_1 N_1 [(I_{E1}/N_1) + [I_{01}/(N_1 + \beta N_2)] - C_1]. \quad (5)$$

Just as for the interference analogue (Eq. (4)),  $d\hat{N}_1/dN_2 < 0$  and  $d^2\hat{N}_1/dN_2^2 > 0$ . The isoclines intersect once and eigenvalues from the linearization are negative real. Hence the single intersection is a stable node. To determine whether the stability applies to all  $\hat{N}$ , we must use Dulac's extension of Bendixson's criterion, since the simple Bendixson criterion is inconclusive. In Dulac's extension, to guarantee no closed trajectories, we need to choose a multiplier  $B(N_1, N_2)$  continuous and with continuous derivatives such that

$$(\partial/\partial N_1)(B dN_1/dt) + (\partial/\partial N_2)(B dN_2/dt)$$

is of constant sign (Andronov *et al.*, 1966). Choice of  $B = 1/N_1N_2$  meets this criterion for the first quadrant.

Thus Eq. (5) behaves very much like (4). The only difference is that in (5) the isoclines merge with nonzero asymptotes, those asymptotes being equal to the number of individuals supportable on the exclusive resources (Fig. 1). Were a refugium to exist from interference, Eq. (4) would look qualitatively very much like (5), though the parameters and variables are related differently (see below).

Because of the nonzero asymptotes, Eq. (5) or (4) with refugia are freed from one unrealistic assumption of the simple version of (4). Eq. (4) assumes that as  $N_2$  increases,  $N_1$  never has its growth rate reduced to zero, because the share of resources per individual,  $I_{E1}/N_1$ , becomes large at a sufficiently rapid rate. However, for  $N_1$  small relative to  $I_{E1}$ , this assumes an unrealistic ability to process food. Hence it is likely that at some point the  $N_1$ -isocline will touch the  $N_2$ -axis (for all practical purposes, it does anyway when  $N_1 < 1$ ). But if the  $N_1$ -asymptote is nonzero, no such unrealistic assumption need be made.

Various more complicated isoclines can be obtained by simplifying the general model with fixed energy input

$$dN_1/dt = R_1N_1[I_{01}/(N_1 + \beta N_2)] + (I_{E1}/N_1) - \gamma_{12}N_2 - \gamma_{11}N_1 - C_1]. \quad (8)$$

This system is structurally equivalent to one where constant and cubic terms are added to Lotka-Volterra. Here we use (8) only to show how interference reduces exploitation (which, as MacArthur (1972) has pointed out, provides the selective motivation for deliberate interference) and thereby transforms (8) into our purer models. Where the  $\gamma_{12}$  term is large (great interference), the most important effect in (8) should be to reduce  $\beta$ , the likelihood of an individual of Species 2 getting an item of overlapping resource relative to an individual of Species 1. Then the first two terms of  $M$  are approximately  $I_1/N_1$  and we have Eq. (4). In contrast, where interference is low, the  $\gamma$  terms drop out and (8) is approximately (5), the pure exploitative model. High interference investment might also result in high death rates. In these ways, the simple models can be used to represent the trade-offs that seem to result from investment in interference (e.g. Pitelka, 1951; Ripley, 1959; Clatworthy and Harper, 1962; Horn, 1971; Recher, 1971).

In summary so far, for the simple models given here, when nonlinear isoclines result, they are always concave. When these isoclines intersect in exactly one way, they give stable coexistence.

Representatives of the five kinds of models can be combined in various ways to give additional cases. The most intriguing such combination models the "included niche" phenomenon, in which one species has its resource set entirely contained within that of another (Miller, 1967). In terms of our models, the situation is represented by Eq. (3) for the included species (Species 2) and Eq. (5)

for the other (Fig. 2). The species with exclusive resources will obviously always survive, but whether the other does or not depends on several parameters. Simple algebra shows that the two isoclines either (1) intersect once in the first quadrant, whence the singularity is a stable node or (2) fail to intersect, resulting

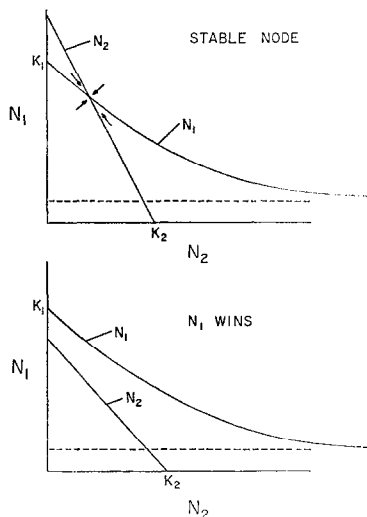


FIG. 2. Competition in included-niche exploitative model.

in exclusion of the included species. Parametric constraints are that  $K_1 < I_2\beta/C_2$  for coexistence or the opposite for exclusion. In words, for coexistence (1) the carrying capacity of the broad-niched species must be small; (2) the feeding efficiency of the included species must be large; (3) the likelihood of the included species getting an item of the overlapping resource must be great; and (4) the death and maintenance rates of the included species must be small.

The dynamical models discussed so far have some major weaknesses. One is the unrealistic assumption certain models (e.g. Eq. (4)) make about the consumption abilities of individuals when population sizes are low relative to food input. A second is the unrealistic one-way interaction of populations and the food supply, whereby the generation of food for the populations per unit time is not affected by consumption. However, if we are only interested in the equilibril properties of populations, these assumptions are not crucial because alternative models without them imply the same zero-isoclines. We now briefly review two classes of such models: first, fixed-consumption models where individuals are limited in consumption abilities; and second, resource-consumer models, where resources act as populations that are dynamically coupled to consumers.



## 2. Fixed-Consumption Models

Our approach in this section will be to construct "consumption" isoclines, giving how many individuals of Species  $i$  can be supported simultaneously with fixed numbers of Species  $j$ . We consider three kinds of partitioning of a fixed supply of resources, only the third of which allows a stable point equilibrium.

### a. One Resource; Species-Specific Consumption

The simplest such model is competition for space, where each species has a fixed territory size and the species are both inter- and intraspecifically territorial (Many such cases are reviewed for birds by Orians and Willson (1964).) Then  $K_i = A/T_i$ , where  $A$  is the area of contention and  $T_i$  is the territory size of Species  $i$ .  $\alpha_{ij}$  is the number of individuals of Species  $i$  an individual of Species  $j$  deprives of space, and that is just  $T_j/T_i$ . Such  $\alpha$ 's imply parallel isoclines for two species, and the  $K$ 's imply that the isoclines are coincident. These arguments obviously hold no matter what the resource is, and if there are several resources with fixed consumption levels of each for both species, point coexistence is likewise impossible (Schoener, in preparation).

### b. Many Resources; Fine-Grained, Species-Specific Consumption

Suppose individuals of both species take resource kinds in proportion to their environmental availability. Let  $b_{ik}$  be the energy extracted by an individual of Species  $i$  from Resource Type  $k$ , and  $Q_i$  be the energy required by an individual of Species  $i$  per unit time (including costs for food search). Then the number of items necessary to support an individual of Species  $i$  per unit time is  $n_i = Q_i / \sum_k p_k b_{ik}$ , where  $p_k$  is the environmental frequency of Type  $k$ . The competition coefficient  $\alpha_{ij}$ , or the number of individuals of Species  $i$  an individual of  $j$  deprives of resources when fulfilling its requirements, is  $n_j/n_i$ . Furthermore, if the maximum number of resource items the populations have available per unit time is  $S$ ,  $K_i = S/n_i$ . Once again,  $K$ 's and  $\alpha$ 's imply coincident isoclines for two competitors and no point equilibrium. In cases (a) and (b), dynamics are not specified, but that species with the greatest reproductive and/or immigration rate will predominate.

### c. Three Resource Kinds; Coarse-Grained, Species-Specific Consumption

Suppose as for Eq. (5) that each species has exclusive resources as well as resources they both consume with relative proportions  $\beta$ . To construct an isocline for Species 1, we imagine it is at the maximum possible number its resources can support and ask what reduction in  $N_1$  various fixed numbers of Species 2 will produce. In that situation, individuals of Species 1 will feed all the time, but

those of Species 2 will feed only in proportion to their fixed level. As Appendix 1 details, the isocline for Species 1 works out as

$$\hat{N}_1 = K_1 - \beta N_2^2 c_1 / ((\beta K_2 N_2 / S) + c_2 \hat{N}_1), \quad (9)$$

where

$$K_2 = \frac{S}{Q_2} \sum_{\substack{\text{all resources} \\ \text{for Species 2}}} p_k b_{2k},$$

$$c_1 = \frac{1}{Q_1} \sum_{\substack{\text{overlapping} \\ \text{resources}}} p_k b_{1k},$$

and

$$c_2 = \frac{1}{Q_2} \sum_{\substack{\text{exclusive resources} \\ \text{for Species 2}}} p_k b_{2k}.$$

But the intersection of the isoclines give values of  $\hat{N}_1$  and  $\hat{N}_2$  that simultaneously satisfy the zero-isocline equations for (5) if  $K_1 = I_1/C_1$  and  $S c_1 = I_{01}/C_1$ . Hence this system is identical to Eq. (5) at equilibrium, even though individuals are assumed fixed in consumption instead of flexible as in (5).

### 3. Two-level Systems

We can give two rather different ways of modeling competition via simultaneous depletion of dynamically changing resource populations. The first has resources growing logistically in the absence of predation (MacArthur, 1968), as in intraspecific interference:

$$\begin{aligned} dN_i/dt &= R_i N_i \left( \sum_k a_{ik} b_{ik} F_k - C_i \right), \\ dF_k/dt &= r_k F_k - (r_k F_k^2 / K_k) - F_k \sum_i a_{ik} N_i. \end{aligned} \quad (10)$$

The second has resources flowing into the system at constant rate, as for example insects immigrating from some external breeding place. Resources disappear either through predation or some death rate that is constant per unit resource:

$$\begin{aligned} dN_i/dt &= R_i N_i \left( \sum_k a_{ik} b_{ik} F_k - C_i \right), \\ dF_k/dt &= S_k - D_k F_k - F_k \sum_i a_{ik} N_i. \end{aligned} \quad (11)$$

For Eqs. (10)–(11),  $F_k$  is the number of individuals of Resource  $k$ ,  $a_{ik}$  is the

consumption rate of Resource  $k$  by Competitor  $i$ ,  $b_{ik}$  is the net energy per item of Resource  $k$  extractable by an individual of Competitor  $i$ ,  $K_k$  is the carrying capacity of Resource  $k$ ,  $r_k$  is the intrinsic rate of increase of Resource  $k$ ,  $S_k$  is the flow of Resource  $k$  into the system and  $D_k$  is the death rate of Resource  $k$ . Other symbols are as above. Stability and positivity of these equations have not been systematically investigated, but Schoener (1973) has discussed their versions for one consumer and one resource, and May (1971) and MacArthur (1970, 1972) comment on the many-species systems.

For our purposes, the equations are of interest mainly at equilibrium. As MacArthur (1968) showed, if the  $F$  equations in (10) are solved for the  $\hat{F}$ 's and these substituted into the equilibrium equations for the  $N$ , linear isoclines in the  $\hat{N}$  result. Hence a purely exploitative system can give rise to linear isoclines, in contrast to our results with one-level dynamical systems above.

Equation (11) on the other hand generates highly nonlinear isoclines. If  $D_k = 0$  for all  $k$ , the degree of the isocline equation in  $\hat{N}_i$  is equal to the number of resources Species  $i$  uses ( $a_{ik} \neq 0$ ). For the two-competitor, three-resource case, where only one of the resources is shared and the others are exclusive to different competitors, the isoclines at equilibrium are identical to those for Eq. (5). Here again then, is an exploitative dynamics giving statics identical to our simplest exploitative model.

### III. TESTING COMPETITION MODELS AND RELATING THEM TO HABITAT SHIFT

#### 1. *A Regression Method*

The most ideal application of our simple competition models is to populations in isolated units of homogeneous space. Such units have been contrived in the laboratory to evaluate both the dynamical and equilibrial predictions of simple models, often with considerable success (Ayala, 1971; Frank, 1952; Gause, 1934; Gill, 1972; Miller, 1964a, b; Park, 1962; Vandermeer, 1969). Application of the models to unmanipulated field situations, however, is necessarily more incomplete and strained. Only the equilibrium forms of the models can be used, and as we have shown, sometimes a variety of dynamics can give rise to a single such form. Furthermore, we hope that the spatial units designated as theaters of competition are sufficiently isolated from other units yet each sufficiently homogeneous to correspond to the model's assumptions. Despite these reservations, the models are, I believe, preferable to arbitrary descriptive models. Not only do they allow preliminary assessment of various kinds of competitive mechanisms, but estimates for biologically interesting quantities are generated that can be independently checked by detailed behavioral and physiological

measurement. We now discuss how competition models at equilibrium can be applied to natural data on relative occurrences of species.

All the zero-isocline equations from the models have the following properties.  $\hat{N}_1$  is explicitly the dependent variable.  $\hat{N}_1$  is a function of (1)  $K_1$ , the carrying capacity of Species 1, (2) competition parameters measuring effects of Species 2 on Species 1, and (3)  $N_2$ , the abundance of the competing species. The carrying capacity of the second species, as well as parameters describing the effects of the first species on the second, do not appear in the isocline equation for Species 1. This means we can test the isocline equations if we can find competition "arenas" between which the equilibrium abundance of the second species,  $\hat{N}_2$ , varies.  $\hat{N}_2$  should vary for fixed  $K_1$  if  $K_2$  varies from arena to arena. Thus by varying the carrying capacity of the second species, we should be able to trace the isocline for Species 1. While varying a single  $K$  at a time seems feasible for laboratory manipulation, finding such situations made to measure in nature may appear harder. However, this is no problem if we are willing to increase the dimensionality of our analysis by considering  $K_1$  as an independent variable additional to  $\hat{N}_2$ . Then instead of testing the shape of a line (one independent variable,  $\hat{N}_2$ ), we are testing the shape of a surface (two independent variables,  $K_1$  and  $\hat{N}_2$ ). Figure 3 illustrates such surfaces for some of our models.

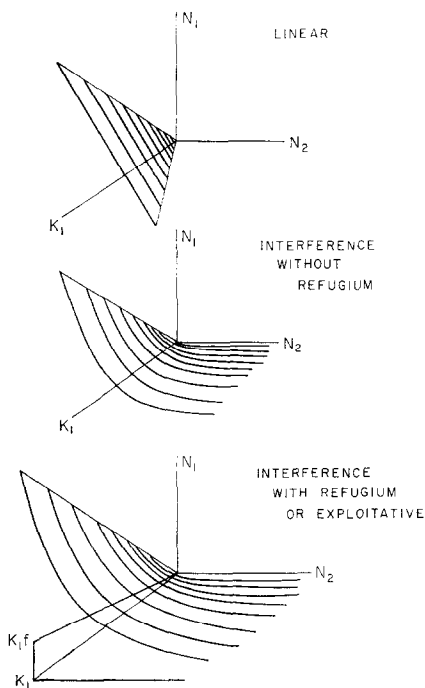


FIG. 3. Competition models in two variables.

The sort of natural units best corresponding to our assumptions are isolated areas of horizontal space, such as islands. However, it is mathematically possible to fit the isocline equations to data from spatially contiguous units such as different habitat types. To do this, consider the habitats as separate arenas indexed by  $h$ . Then we can use the data vector  $\langle \hat{N}_1, \hat{N}_2, K_1 \rangle_h$  as variables in a regression equation and estimate, by a least-squares linear or some nonlinear technique, the competition parameters as regression coefficients. In other words, each habitat  $h$  gives a point in  $(\hat{N}_1, \hat{N}_2, K_1)$ -space, and we try to fit the isocline equations to that collection of points by varying parameters. In so doing we assume that the carrying capacity for each habitat can vary while the interspecific competition parameters stay constant. In some models such as Eqs. (3) and (5), the assumption is theoretically entirely consistent; the carrying capacity of Species 1 does not contain the interspecific competition parameter or factors of it. In Eq. (4), the quantity  $1/C_1$  is a factor in common, but most components are not shared. However, there are other equations where parameters are more confounded. For example our version (Eq. (2)) of the Lotka-Volterra system (1) shows that  $K$ 's and  $\alpha$ 's are composed of mostly the same parameters. The only parameter in  $K$  not in  $\alpha$  is  $C$ . However,  $E$ , which measures the feeding rates and which is the most important term in the expression for  $K$ , appears in that expression asymmetrically in the numerator and denominator, while in  $\alpha$  it appears multiplied by and added to terms of the same order. Therefore, variations in  $E$  should affect  $K$  more than  $\alpha$ . Similarly in MacArthur's system (10) at equilibrium,  $K$  and  $\alpha$  contain the same parameters except for  $C$  and the  $a$ 's of the competitor. Again, symmetry implies that variation in the  $a$ 's,  $b$ 's,  $K_k$ 's or  $r_k$ 's should affect  $K$  more than  $\alpha$ . Indeed, Gill (1972) has empirical evidence for the constancy of  $\alpha$  relative to  $K$  for *Paramecium*.

Our regression approach assumes equilibrium is reached separately in each habitat. The dynamics are not specified and certainly will often be quite unlike those given by the simple models. However, at equilibrium the models all give isoclines which are rearrangements of the expression  $M(N_1, N_2) = 0$ , where  $M$  is the per-unit-time energy input per individual after deletion for maintenance, activity and replacement. Hence the method only assumes that a habitat neither gains nor loses individuals once the energy collected in that habitat by an individual just balances energy lost (see Section III-3). The method does make the strong assumption that interchange of individuals between habitats does not cause some to be overused and others underused.

## 2. Comparison with "Overlap" Measures of Competition

The regression method contrasts markedly with that proposed in MacArthur and Levins (1967), Levins (1968) and MacArthur (1968) for estimating competi-

tion coefficients, those parameters incorporating intensity of inter- vs intraspecific competition. The MacArthur-Levins ( $M-L$ ) method for habitats uses

$$\alpha_{12} = \sum_h p_{1h} p_{2h} / \sum_h p_{1h}^2, \quad (12)$$

where  $p_{ih}$  is the utilization frequency of the  $i$ th species for habitat  $h$ . The regression method for linear isoclines fits data to the multiple-regression equation

$$\begin{aligned} (\hat{N}_1)_h &= (K_1)_h - \alpha_{12}(\hat{N}_2)_h \quad \text{implies} \\ p_{1h} &= k_1(K_1)_h + k_2 p_{2h}. \end{aligned} \quad (13)$$

In the bottom version of (13),  $k_1$  and  $k_2$  are the regression parameters resulting from converting the top version into dimensionless form;  $-k_2$  is directly proportional to  $\alpha$ . Equation (13) is only appropriate where isoclines are linear, and there are as many alternative equations as there are reasonable combinations of reasonable independent variables (see below).

There has recently been some question as to whether the  $M-L$  measure (essentially a one-sided indicator of niche overlap) is in fact a suitable measure of competition (Vandermeer, in seminar, 1972; Trivers and Nisbet, manuscript; Colwell and Futuyma, 1971). An argument against using  $M-L$  is that species showing a low coefficient may have responded to past competitive events by one or both being forced out of each other's prime habitats. Conversely, a high  $M-L$  coefficient may indicate that the species in fact do not compete. To discover what is going on, the argument continues, one must compare niches of species in the absence of competition with niches in its presence, i.e., one must compare the fundamental with the realized niche (sensu Hutchinson, 1957). It may seem disturbing that there could be controversy over so basic a question. However, the regression method gives a possible formalism for incorporating the arguments just presented. Relative  $(K_1)_h$  in Eq. (13), as detailed below, might be considered the species' relative utilization in its fundamental niche, whereas relative  $(\hat{N}_1)_h$  is its relative utilization in some realized niche. The regression method compares  $(\hat{N}_1)_h$  with  $(K_1)_h$  and scales the competition parameter accordingly. Comparing the  $M-L$  (Eq. (12)) with the regression (Eq. (13)) method shows that, rather than a conflict in logic, the methods make basically different assumptions about the kind of competitive system being studied. We now discuss these differences.

The most important difference concerns what constitutes a resource. The only lower-level justification for the  $M-L$  equation is MacArthur's (1968, 1972), which shows that the consumer-resource equations (10) give at equilibrium

$$\alpha_{ij} = \left( \sum_k a_{ik} a_{jk} b_{ik} K_k / r_k \right) / \left( \sum_k a_{ik}^2 b_{ik} K_k / r_k \right).$$

This equation is quite general and applies to any resource kind. When resources are equal in their  $K/r$  and  $b$ , these factors drop out. However, to substitute  $p$ 's for  $a$ 's so as to get (12), is to assume that the per-item propensity of consumption (the  $a$ 's) is proportional by the same factor to actual consumption or utilization (the  $p$ 's). MacArthur argues that this should be so for similar consumers where the resource kinds are in one-to-one correspondence with habitat kinds, i.e., the  $k$  and  $h$  both index habitats. Then the time spent in each habitat (proportional to  $p$ ) is proportional to the likelihood of consuming an item of resource in that habitat. Where the resources are not habitats, but rather sizes or species of prey, Eq. (10) implies that utilization (e.g. percent in gut contents) cannot be used in (12), but electivities must be substituted for the  $p$ 's (the argument is detailed in Schoener, 1974). For present purposes, the important point is that where resources are items in particular habitats and behave as in (10), spatial overlap necessarily implies overlap in resource utilization and thereby exploitative competition.

The regression method, in contrast, makes no one-to-one identification of resources with habitats. Rather, habitats are considered simply the arenas in which competition takes place. In fact for equilibrium to be stable within a habitat, that habitat must contain heterogeneous resources if resources are limiting. For example resource kinds may be food sizes and the outcome of competition may depend on how similar species are in the sizes of foods they eat, as well as on the production of the various food sizes in each habitat. In contrast to the indirect linkage of habitats via consumer consumption in (10), the regression method assumes no linkage whatever. Within each habitat however, any kind of competition including all those modelled above can take place. In fact (10) could hold independently within each habitat and for any kind of resource.

Because of differences in assumptions on what the resources are and how the various habitats interact, the two methods necessarily compute competition parameters differently. The M-L method measures competition by directly measuring overlap in the resources, which for MacArthur's system are the habitats. The regression method estimates competition indirectly; it compares the competitor-laden with the competitor-free state to calculate its intensity. That intensity in turn may be determined by resource overlap, aggression or some other kind of competition. Consequently, when the habitat preferences of the species are different, the M-L method necessarily gives a low competition parameter, whereas the regression method may give a high competition parameter, but need not, depending on the distribution of the  $K$ 's. If the  $K_h$  are such that the species should overlap greatly, then the competition parameter will be high. In contrast, when the habitat preferences are relatively alike, M-L necessarily gives a high parameter, whereas regression could easily give a very low parameter. It may even give a parameter ( $k_2$  in Eq. (13)) of positive instead

of negative sign. In that case, what is indicated is that the species are not competing much, perhaps because they eat different foods, but they do prefer the same habitats.

The competition parameter  $\alpha$  as given by (12) can be plugged into an isocline equation to calculate the total abundances of the species in all habitats combined. This is only possible for the regression method when isoclines are linear as in (13). Then if  $\alpha$  is constant throughout all habitats, we can sum the first version of (12) over all  $h$  to get  $\sum_h (N_1)_h = \sum_h (K_1)_h - \alpha_{12}(\hat{N}_2)_h$ , implies  $\hat{N}_1 = K_1 - \alpha_{12}\hat{N}_2$ , where the variables in the latter expression are totals. Incidentally, if the  $\alpha$ 's are habitat-specific, similar algebra shows that the  $\alpha$  giving the total  $\hat{N}_1$  is a weighted average of the separate  $\alpha$ 's, where the weighting factors are the relative abundances of Species 2. In symbols,  $\alpha_{12} = \sum_h (\alpha_{12})_h [(\hat{N}_2)_h / \hat{N}_2]$ .

It is important to realize that our regression method is not a completely general way of incorporating alternatives to M-L. For example species upon coming together may displace in food sizes. Such displacement should involve morphological change. It implies that instantaneous competition, as measured by M-L, becomes slight. Comparing the fundamental and realized niches along the food-size dimension then indicates the intensity of past competition. If the species evolutionarily diverge in habitat preference and the items in habitats correspond to resource kinds, then instantaneous competition again becomes low. In neither case does the regression method as conceived here apply. But if the habitats characterize the arenas rather than the objects of competition, then we can use habitat cooccurrence to tell us via the regression method how intense the competition is, whether it be interference or exploitation.

### 3. *Category Choice*

A difficult operational problem for habitat analyses is category choice. The selection of categories for "niche" analysis has always been a *bête noire* for community ecologists. It plagues not only ecologists interested in the biological reality of categories but also statisticians interested in problems of how to group continuous data for discrete analysis (e.g. Fienberg, 1970). Obviously for any set of nonuniformly distributed data, how one delineates categories is going to affect estimates for parameters.

For data distributed over a set of habitat axes such as vegetation height and diameter, the biologically traditional way to define habitats is to break the data at places where those data show the steepest gradients. Indeed, to the degree that there are no differences in gradients for the variables of interest, the habitats are arbitrary. Such gradients may reflect ways the consumers perceive or react to the habitat variables or how strongly connected the resources are within various units of space. Conceivably, such properties of consumers or their resources can be extremely location-specific, so much so that they are adequately described by



continuous functions. Then calculation of such quantities as consumer abundance requires evaluation of integrals involving combinations of these functions. To perform this evaluation numerically, the best procedure is often to break the integral where the integrand changes its value most rapidly, that is, where gradients are steepest. Thus the biologically customary way to define habitats also has mathematical virtues.

#### IV. A PARTICULAR APPLICATION TO LIZARD STRUCTURAL HABITATS

##### 1. *Animals and Localities*

The diurnal, arboreal lizards of the West Indies, especially those of the genus *Anolis*, provide an excellent natural laboratory to search for habitat shift. There are several widespread species that occur with a large number of combinations of sympatric congeners; three of these also occur in a completely solitary state. The data used here were collected at 20 localities from the eastern Caribbean covering most species combinations (described in Schoener, 1975). Additional to geography, anoles are favorable subjects because of ease of observation; they are dense and conspicuous. Furthermore, especially on small islands, these predatory animals are close to the top of the food chain and are therefore likely to be regulated by competition (Hairston, Slobodkin and Smith, 1960).

The particular kind of habitat chosen for this study is the structural habitat (Rand, 1964), a characteristic that has been very useful for discriminating species as well as age and sex classes within species. Structural habitat refers primarily to the heights and diameters of an individual's perches. Structural habitat is highly measurable, not only in terms of the distribution of the lizards themselves, but also in terms of the availability for the lizards of the various categories of perches. One way in which relative availability of the habitats can be measured is in units of surface area. Surface area is, as we have seen, incorporated into that parameter determining interaction frequency for a whole class of interference models. Thus not only can surface area be used in the estimation of relative carrying capacity, as we shall demonstrate, but it is demanded by certain models to predict the intensity of competition by interference.

Despite these favorable aspects, *Anolis* structural habitats are in some ways not ideal for analyzing habitat shift as proposed here.

First, structural habitat is only one way to characterize the habitat surface upon which lizards move. Microclimate is sometimes important and independent of structure (Schoener, 1970; Schoener and Schoener, 1971a, b; Sexton, in preparation), so that changes not ascribable to competitors may be caused by climatic variation. Additionally, the same structural habitat may vary in productivity between localities; for example differences in wind may produce

differences in insect availability on exposed twigs. Plant toxicity may also be important. But to consider jointly these other habitat characteristics would be to introduce variables far harder to measure than structure, even though the latter has some drawbacks (Andrews, 1971; Schoener and Schoener, 1971a).

Second, habitats and lizards may not behave as in our ideal for application of the regression method. Resources may not renew independently in the separate habitats. Further, we are assuming that the placement of the habitats does not prevent the number of lizard hours spent in a particular habitat from being that exactly balancing energy loss and gain. But some habitats are no doubt used as way stations between others providing richer food. In other words, animals may be willing to incur a metabolic loss in a habitat providing access to another that gives a gain.

Third, we are assuming that the animal's behavioral and genetical systems can discriminate habitats with respect to energy yield and can balance time budgets accordingly. Again this limitation could cause animals to occupy a habitat to the extent that the loss there outweighs the gain.

Finally, recall we are assuming  $\alpha$  constant but  $K$  variable between habitats. This implies that habitat structure should be more correlated with productivity and feeding efficiency than with interference losses or relative competitive abilities in appropriating items. Because the first pair involves both environmental availability and individual abilities while the second involves only the latter, the assumption may often be reasonable. However, the animals do differ in size and body proportion, and these differences should result in different relative competitive abilities that correlate with different perch structures. For example large lizards are not usually going to be as adept as small lizards in catching prey on small perches. However, without making the assumption that the correlation of competitive ability and habitat structure is low, we cannot fit parameters by our regression method at all. Of course if the competition coefficients are measured separately as in behavioral studies, our models can be applied habitat-by-habitat to portray the overall form of habitat shift.

## 2. *Methods*

### a. *Data and Categories*

i. *Lizards.* Observations are gathered by walking through the study area and recording the initial perch height and diameter of every lizard seen (reviewed in Rand, 1964; Schoener and Schoener, 1971a). Observations therefore correspond to points in time and, when summed over the entire activity period, represent the long-term distribution of the population over the structural habitat categories. The number of observations per lizard species varied from 300 to over 1000 (mean c 600). These records, when converted into frequencies, do

estimate the relative number of "lizard hours" logged by the population in the various microhabitats, just the quantity we need to apply the methods outlined above.

ii. *Vegetation.* The relative availability of the microhabitat categories was measured in the following way.

For randomly chosen sections of the study area, measurements were made at 6–8 different heights in the vegetation of the diameters of all branches and twigs ( $> 1/8$  in.). The normalized distribution for each height can be thought of as a conditional probability distribution of diameter, given a particular height. We can then use these conditional distributions to estimate the joint probability distribution of height and diameter, where what is being measured is the number of vertical positions available for a lizard within a certain height–diameter category. This was done simply by assuming that the number of such positions is proportional to the size of the height interval for the category, and then evaluating the areas of a set of trapezoids corresponding to approximation of various definite integrals of the relevant conditional probability density. This joint distribution gives the relative availabilities that we need.

However, this method does not estimate surface area. Therefore for each branch or twig, the angle of inclination with respect to the vertical,  $\theta$ , was recorded, since the more horizontal a branch is within a given height interval, the more surface area it has within that interval. Each diameter observation was then weighted by  $\sec \theta$  as well as by the actual value of the diameter, and these were summed to give a new distribution for each height sampled. Then the joint distribution was estimated as before to give relative surface area.

iii. *Categories.* Category choice must strike a balance between partitioning too fine, which can give noisy results, and partitioning too coarse, which can obscure differences. For these data, trial and error indicated that about 40–50 observations per category gave the most striking patterns. Various combinations of boundaries were tried and four selected (Schoener, 1975, gives sets used; sets tried available upon request). Two of these divided observations by height alone and two were jointly determined by height and diameter. Within each type, one category-set subdivided the upper and one the lower vegetation more finely. The latter distinction provided sets sensitive to changes in canopy and understory species, respectively. However, consistency was preserved by using each of the four sets for each species.

#### b. *Data Vectors and their Incorporation into Models*

Two kinds of data vectors are used in this study.

*Allopatric-sympatric* data have as dependent variable  $S_s$ , the frequency of the given species (or species class) where it occurs with competitors, and as inde-

pendent variables (before consolidation into fewer independent variables) (1)  $S_A$ , the frequency of the given species where it occurs without competitors, (2)  $S_C$ , the frequency of the competing species (one or more), (3)  $H_A$ , the frequency of the vegetational habitat where the given species occurs alone, and (4)  $H_S$ , the frequency of the vegetational habitat where the given species occurs with competitors. Each of these frequencies is calculated for each habitat category. These data allow comparison of the structural habitats of a given species where it occurs alone, corresponding to a slice of Hutchinson's (1957) fundamental niche, and where it occurs with competitors, corresponding to a slice of Hutchinson's realized niche.

*Sympatric-sympatric* data vectors allow comparison of the habitats of populations from a given species inhabiting two localities at both of which there are competitors. There are now six variables,  $S_{S1}$  and  $S_{S2}$ , the frequency of the given species in Localities 1 and 2, respectively,  $S_{C1}$  and  $S_{C2}$ , the corresponding frequencies for competing species, and  $H_{S1}$  and  $H_{S2}$ , the frequencies of vegetation. In this situation there are two candidates for the dependent variable,  $S_{S1}$  and  $S_{S2}$ . Because there is no a priori reason to select one over the other, both were always used. If the data are perfectly fitted by a model, this procedure would be redundant, since parameters calculated from the regression of  $S_{S1}$  could be used to derive exactly those for the regression of  $S_{S2}$ . But of course models never fit data perfectly, so the two kinds of regressions give different estimates.

We now show how the above variables are translated into those in the isocline equations.

In all the competition models of Section II, carrying capacity is directly proportional to the surface area of the vegetation, assuming (1) number of interactions per unit time is inversely proportional to the area over which the interactions take place and (2) productivity of food within each kind of microhabitat is directly proportional to surface area. For Eq. (2),

$$K_1 = (E_1 - C_1)/(\gamma_{11} + \lambda_{11}E_1).$$

Since both  $\gamma_{11}$  and  $\lambda_{11}$  are inversely proportional to surface area,  $K_1$  should increase directly with surface area. For Eq. (10),

$$K_i = \left( \sum_{k=1}^m a_{ik} b_{ik} K_k - C_i \right) / \left( \sum_{k=1}^m a_{ik}^2 b_{ik} K_k / r_k \right).$$

Each  $a_{ik}$  is inversely proportional to surface area and each  $K_k$  should be directly proportional to surface area. Thus surface area cancels out of the numerator and appears once in inverted form in the denominator, so  $K_i$  is directly proportional to surface area. For Eqs. (3), (4) (with  $\gamma_{11} = 0$ ), (5) and (11) (with  $D_k = 0$ ),  $K$  is energy input to the consumer populations divided by a per indi-

vidual maintenance-and-replacement rate; the numerator should directly increase with increasing amount of habitat. For Eq. (4),

$$K_1 = (-C_1 + (C_1^2 + 4\gamma_{11}I_{E1})^{1/2}/2\gamma_{11},$$

since  $\gamma_{11}$  is inversely and  $I_{E1}$  directly proportional to surface area,  $K_1$  is directly proportional to surface area.

For allopatric-sympatric data, that  $K$  is directly proportional to surface area means that  $K$  for habitat category  $h$  can be estimated as  $(S_A^*H_S^*/H_A^*)_h$ .<sup>2</sup> That is, the ratio  $S_A^*/H_A^*$  gives the number of individuals of the given species per unit habitat for Category  $h$  in a locality where the given species occurs alone. Assuming this ratio is a species-specific characteristic, determined by properties of the vegetational structure and the animal living on it, the number of individuals expected in Locality  $S$  were there no competitors is just the ratio times  $H_S^*$ .

To the degree that species change their abilities on different kinds of vegetational structure between localities, this estimation of carrying capacity is inadequate. Differences in such abilities have never been directly measured, but two morphological characteristics that would be expected to be correlated with them are overall size and limb-trunk proportions. Size does change from island to island within a given species, sometimes in a regular manner (Schoener, 1969). Similar changes in proportion have never been carefully looked for. However, for two species color and pattern change drastically from one island to the next (Schwartz, 1968; Schoener, 1975). In *carolinensis* and to a lesser extent *distichus*, these color changes parallel shifts in the kinds of vegetation frequented and seem adaptive for purposes of concealment. Such color changes may thereby lower mortality and raise feeding success differently in the different habitats. What this means is that estimates for  $K$  may be too low in places where the given species is common and too high in places where it is rare. The net result can be estimates for the competition parameters that are too high, at least inasmuch as they measure instantaneous competition. These high parameters, however, do indicate that past competition was severe.

Translation of isocline equations into those involving data variables is now straightforward. For example the linear model (13) becomes

$$(S_S^*)_h = (S_A^*H_S^*/H_A^*)_h - \alpha_{12}(S_C^*)_h. \quad (14)$$

Rather than use absolute numbers, this expression and corresponding non-linear ones were transformed into equations using dimensionless variables so that frequencies could be used instead. This is because our lizard censusing technique gives an accurate picture of the relative number of lizards in the

<sup>2</sup> Asterisks denote absolute numbers whereas unmodified symbols refer to frequencies, as defined above.

different habitat categories but not the absolute number per unit surface area. To obtain the latter kind of data would require that animals be "marked out" in the study areas so as to determine how many individuals were actually being counted.

Use of frequencies means that the equation contains, as additional parameters or factors of original parameters, ratios of the abundances of lizards and habitats. Define  $N_S$ ,  $N_A$  and  $N_C$  as the absolute numbers of lizards summed over all  $h$  for the sympatric population, the allopatric population and the competitor population, respectively. Also define  $A_A$  and  $A_S$  as the total number of habitat units from Locality  $A$  and  $S$ . Then  $S_S = S_S^*/N_S$  and similarly for the other frequencies so that (14) becomes

$$(S_S)_h = ((N_A/N_S) \cdot A_S/A_A) \cdot (S_A H_S/H_A)_h - \alpha_{12}(N_C/N_S)(S_C)_h. \quad (15)$$

Notice that we pick up a degree of freedom, since the relative carrying capacity  $(S_A H_S/H_A)_h$  has before it a factor which is the ratio of the per-unit-area abundances.

In short, the kind of model just described measures, by fitting interaction parameters, the degree of habitat shift due to competition. It does this by comparing  $(S_S)_h$  to  $(S_A H_S/H_A)_h$  or the actual habitat utilization to that expected on the basis of vegetational differences alone. Figure 4 gives an example.

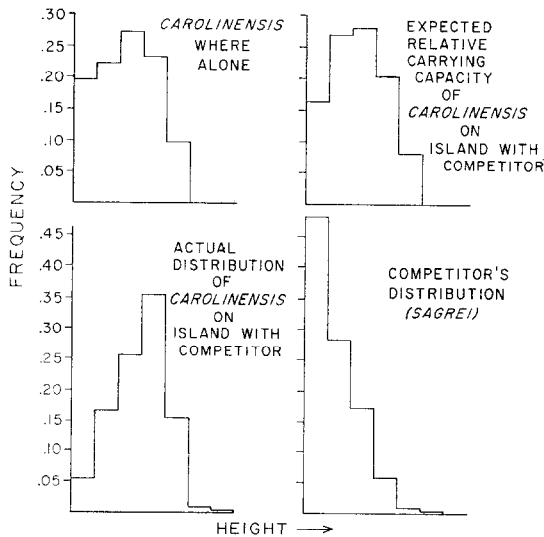


FIG. 4. Shift in height of *Anolis carolinensis* on Crooked Island. Expected distribution computed on basis of *carolinensis* where alone on Acklins Island, corrected for habitat differences between Acklins and Crooked.

Table 1 lists the nonlinear isocline equations used as models for fitting allopatric-sympatric data. The equations are given in terms of the variables listed above and the parameters built from the various competition and abundance constants:

Model 1 corresponds to Eq. (4)'s isocline, where  $\gamma_{11} = 0$ . Since  $\gamma_{12}$  is proportional to the likelihood of encounters, it is inversely proportional to surface area. Hence a dimensionless density of competitors,  $S_C/H_S$ , appears in the isoclines.  $I_E$  is a proportionality factor incorporating the energy per interspecific interaction (also in  $\gamma$ ) and  $C$ .

Model 2 is one of the simplest arbitrary nonlinear forms, where  $\mu$  is the competition parameter. It is similar to Model 1 (and identical through terms of first degree in a MacLaurin expansion in two variables). The expression is easier to analyze numerically than Model 1 however, because it lacks that model's discontinuities in parameter space. It too contains  $S_C/H_S$  rather than  $S_C$ . Tests on Models 1 and 2 indicate that per-unit-area abundance gives substantially better fits to data than abundance alone. For Model 1, 71 % of 214 cases were fit best using  $S_C/H_S$ ; for Model 2, 60 % of 147 cases were fit best using  $S_C/H_S$ . This result increases our confidence in the lower-level derivation of Model 1.

Model 3 is Model 1 with a refugium from interference tacked on;  $f$  is the fraction of  $K$  supportable by that refugium.

Model 4 is Model 2 with the same refugium.

Model 5 is a form which can generate convex downward models; it will if  $\rho > 1$ . For the nonlinear regressions,  $\rho$  was started at 2 so that the model would have a chance to converge on a convex form if the data favored this. A crude a posteriori interpretation of this model with  $\rho = 2$  is that  $\alpha_{12}$  in a linear form is proportional to Species 2's population size with factor  $\nu N_C$ , as if that size in turn were proportional to a habitat-specific superiority of Species 2.

Model 6 is the full isocline equation for (4), where  $\gamma_{11} \neq 0$ .  $I_A$  is the intraspecific proportionality factor corresponding to  $I_E$ . Notice that  $K_1$  does not appear in the isocline equation although its components do. This is unlike the linear case where the  $K$ 's appear intact. In both linear models and Eq. (4) there is a trade-off between population reduction entailed by interspecific interference and that from intraspecific interference. But in linear models this trade-off can be expressed in units of either of the two species, since for all values of  $N_1$  and  $N_2$  the ratio of deleterious effects stays constant; in economic jargon they are "perfect substitutes." No such constancy exists for the nonlinear isoclines of (4).

Model 7 is the isocline equation for (5) or a specific version of (11). Here  $f$  is the fraction of  $K_1$  supportable on the exclusive resources.

TABLE 1  
Models for Allopatric-Sympatric Isoclines<sup>a</sup>

1. *Simple interference* (no tradeoff, no refugium) (Eq. (4)).

$$(S_S)_h = \frac{k_1(H_S S_A / H_A)_h}{1 + k_2(S_C / H_S)_h}, \quad k_1 = A_S N_A / A_A N_S, \\ k_2 = I_E N_C / A_S.$$

No restrictions on sign.

2. *Simple exponential* (no refugium).

$$(S_S)_h = k_1 \left( \frac{H_S S_A}{H_A} \right)_h e^{-k_2(S_C / H_S)_h}, \quad k_1 = A_S N_A / A_A N_S, \\ k_2 = \mu N_C / A_S.$$

3. *Interference with refugium.*

$$(S_S)_h = \frac{k_1(H_S S_A / H_A)_h}{1 + k_2(S_C / H_S)_h} + k_3 \left( \frac{H_S S_A}{H_A} \right)_h, \\ k_1 = (A_S N_A / A_A N_S)(1 - f), \quad k_2 = I_E N_C / A_S, \quad k_3 = (A_S N_A / A_A N_S)(f). \\ k_3 \text{ restricted to nonnegative values.}$$

4. *Exponential with refugium.*

$$(S_S)_h = k_1 \left( \frac{H_S S_A}{H_A} \right)_h e^{-k_2(S_C / H_S)_h} + k_3 \left( \frac{H_S S_A}{H_A} \right)_h, \\ k_1 = (A_S N_A / A_A N_S)(1 - f), \quad k_2 = \mu N_C / A_S, \quad k_3 = (N_A / A_A N_S)(f), \\ k_3 \text{ restricted to nonnegative values.}$$

5. *Convex.*

$$(S_S)_h = k_1 \left( \frac{H_S S_A}{H_A} \right)_h - k_2(S_C)_h^{k_3} \\ k_1 = A_S N_A / A_A N_S, \quad k_2 = \nu N_C / N_S, \quad k_3 = \rho. \\ \text{No restrictions on sign.}$$

6. *Interference with tradeoff* (Eq. (5)).

$$(S_S)_h = \frac{1}{2} \left\{ -k_1(H_S)_h - k_2(S_C)_h \right. \\ \left. + \left( (-k_1(H_S)_h - k_2(S_C)_h)^2 + 4k_3^2 \left( \frac{H_S S_A}{H_A} \right)_h^2 + 4k_3 k_1 \left( \frac{H_S^2 S_A}{H_A} \right)_h \right)^{1/2} \right\} \\ k_1 = A_S / I_A N_S, \quad k_2 = I_E N_C / I_A N_S, \quad k_3 = A_S N_A / N_S A_A. \\ k_1, k_3 \text{ restricted to nonnegative values.}$$

7. *Exploitative* (Eqs. (5, 11)).

$$(S_S)_h = \frac{1}{2} \left\{ k_1 \left( \frac{H_S S_A}{H_A} \right)_h - k_2(S_C)_h \right. \\ \left. + \left( \left( k_1 \left( \frac{H_S S_A}{H_A} \right)_h - k_2(S_C)_h \right)^2 + 4k_1 k_2 k_3 \left( \frac{S_C H_S S_A}{H_A} \right)_h \right)^{1/2} \right\} \\ k_1 = A_S N_A / A_A N_S, \quad k_2 = \beta N_C / N_S, \quad k_3 = f. \\ k_1, k_2 \text{ restricted to nonnegative values. } 0 < k_3 \leq 1.$$

<sup>a</sup> In all expressions,  $(S_S)_h$  is the dependent variable, other quantities subscripted with  $h$  are independent variables, and the  $k$ 's are parameters to be estimated.



Certain of the models have parameters with signs restricted to positive values (Table 1). This sign restriction was made whenever (1) parameter search may have led to fractional powers of negative numbers or (2) parameter search may have converged on values producing a model where  $S_s$  is a discontinuous function of  $S_c$ , as in Model 1. Hence parameters in the linear model were never restricted in sign. When parameters are not so restricted, we can see whether  $S_s$  and  $S_c$  are negatively related, that is, related as the theory would predict if they are competitors. This gives a qualitative statement about the likelihood of niche shift being caused by competition. A positive relationship could indicate that competition is not great or that the estimate for relative carrying capacity is not very good. In the latter case the abundance of another lizard species is a better predictor of where a given species should be in the vegetation than is  $S_A H_s / H_A$ .

### c. *Species Investigated and Numerical Analysis*

The first step in data analysis was to run least-squares linear regressions considering competitors one at a time (as in Eq. (13)) or jointly per locality. All possible combinations for the three most widespread species were used in allopatric-sympatric regressions using all four category sets. In addition, sympatric-sympatric regressions were run for most combinations of the three most widespread species, as well as for two others never occurring allopatrically. Finally, allopatric-allopatric regressions to test carrying capacity estimates were also run; these have the form

$$(S_{A1})_h = (N_{A1}A_{A2}/N_{A2}A_{A1})(S_{A2}H_{A1}/H_{A2})_h. \quad (16)$$

For the lizard variables, regressions were run with all individuals in a species combined as well as separately for each of two intraspecific classes, adult males and female-sized individuals. These classes are largely discrete because of the great sexual dimorphism in size in the *Anolis* studied; most of the female-sized individuals were adult females but some were subadult males.

Linear regressions are far cheaper to perform than nonlinear ones, so that they serve to screen the enormous number of combinations for groups especially appropriate for nonlinear testing. Seventeen such groups containing 533 cases were selected for allopatric-sympatric regressions (Table 4). They provide an equitable representation of the species classes and category sets and give a substantial number of regressions where the sign of the interaction coefficient is negative.

Three nonlinear treatments were used.

First, for each nonlinear model Raduchel's (1970) program RAPE (Regression Analysis Program for Economists) fitted parameters to each data vector. His algorithm is based on Davidon's (1959) variable-metric technique for minimization with modifications suggested by Fletcher and Powell (1963) and Stewart

(1967). The algorithm begins with user-produced starting values for the parameters and successively changes the parameter values until a minimum sum of squares of residuals (SSQR) is found. Starting values were selected to be numerically and, if possible, biologically reasonable and were the same for each data vector. Convergence was generally achieved with these starting values. It is important to realize that the minimum is not necessarily the global minimum; the surface of the function relating SSQR to the fitted parameters may be bumpy, and this routine is designed to locate that minimum closest to the parameter starting values. Hence the nonlinear models fit at least as well as the regression algorithm calculates. On the other hand the linear models can fit no better or no worse than given by the least-squares method; that method with certain assumptions calculates maximum likelihood parameters for the linear equation, parameters which have been analytically shown to minimize SSQR globally (Draper and Smith, 1966).

Second, ad hoc starting values were used in RAPE for all but Model 5. These were generated by manipulating the models until a linear form in some set of variables resulted. The linear forms were used in ordinary least-squares regression to calculate regression coefficients (and intercepts where appropriate). Pulling apart and piecing together such coefficients to get the parameters of the original models furnished a new set of starting values for each data vector and model. The degree to which the tailor-made and standard starting parameters gave the same final result varied greatly with the model; in general the exponential forms were most stable and the interference models and to a lesser extent the exploitative model were least stable (details of this analysis available upon request).

Third, a very different nonlinear estimation procedure, that of Marquardt (1963), was used with the ad hoc starting values to see to what extent the different routines, when started at the same place, would end with different minima of SSQR. The program employed is based on that given by Conway, Glass and Wilcox (1970) and was extensively modified by David H. Schmalz. In a preliminary trial involving 20 % of the data, the two routines gave virtually the same results in nearly all cases for the 2-parameter models. The 3-parameter models, however, did give different results in a substantial number of cases. This resulted in the decision as to best model being changed only 11 % of the time, however. Though there was little tendency for one or the other routine to do consistently better, the Marquardt routine had the edge and it nearly always converged. However, just like the Raduchel-Davidon procedure, the global minimum SSQR was definitely not reached in some cases. As a result of this preliminary trial, all regressions in all data blocks were run again for the 3-parameter models (including the convex with fixed starting values), this time using Marquardt.

That SSQR used to compare the various models below was the lowest generated by the various approaches.

### 3. Results and Discussion

#### a. Carrying Capacity Estimates

To test the adequacy of the estimate ( $S_A H_S / H_A$ ) for the relative carrying capacity, all possible combinations of solitary species populations were used in allopatric-allopatric regressions (Eq. (16)). If the estimate works, prediction of a species' habitat where solitary by knowing what it does in another locality and knowing the habitat availabilities should average as good as prediction of that species' habitat where nonsolitary. In the later case we know the above information as well as the habitat distribution of the competitor. Therefore we compare goodness of fit (using  $R^2$ , the coefficient of determination) for solitary and non-solitary populations belonging to the same species. We would expect for a given solitary population that  $R^2$  in allopatric-allopatric regressions should be worse than in allopatric-sympatric regressions about 50 % of the time. In fact, average allopatric-allopatric values for a given data block are not too far from 50 % in most cases, but are somewhat more (Table 2). This is not surprising on solely numerical grounds because the allopatric-allopatric regressions have one less free parameter. A biological reason for the percent being more is if prediction of the best habitats is inadequate from comparative vegetation structure alone but

TABLE 2  
Allopatric-Allopatric Compared to Allopatric-Sympatric Data

Pairwise locality comparison	percent times <i>a-a</i> regressions fit more poorly than <i>a-s</i> regressions
<i>Grahami</i>	
GC1 × GC2	54
GC1 × B1	65
GC2 × B1	68
<i>Sagrei</i>	
CB1 × CB2	17
CB2 × A1	83
CB2 × A2	88
CB2 × A3	61
A1 × CB1	57
A1 × A2	49
A1 × A3	63
A2 × A3	47
CB1 × A2	67
CB1 × A3	44

\* GC = Grand Cayman, CB = Cayman Brac, B = Bermuda,  
A = Abaco.

also requires information on the habitats of a noncompeting sympatric species (see below).

The distribution of good and bad fits reveals in part what assumptions embodied in the simple estimation procedure for  $K$  are being violated. In general the regressions fit best (1) localities within the same island and (2) small-sized individuals. The first suggests that microclimate plays an important role additional to that of vegetation structure in determining lizard habitats; islands from different latitudes have different climatic characteristics for the same vegetation structure (elaboration in Schoener, 1975).

The allopatric-allopatric regressions can be used for another purpose; namely to discover which of our two measures of habitat availability, vertical position or surface area, is best for predicting relative carrying capacity. Results from a reduced set of comparisons for each of the two measures show that surface area is far better to use in carrying capacity estimations (Table 3). This is as expected from the theory.

TABLE 3  
Habitat by Surface Area vs Habitat by Vertical Position

Species class	Times best fit <sup>a</sup>	
	area	position
large <i>gambelii</i>	5	1
small <i>gambelii</i>	6	0
large <i>sagrei</i>	16	3
small <i>sagrei</i>	10	7

<sup>a</sup> Using  $R^2$  to 2 significant figures.

#### b. Allopatric-Sympatric Data

We rank the various models according to goodness of fit in two ways.

First, consider all models together and select the best model for each case (Table 4). This is done with and without inclusion of the linear models. If the best model for a particular case turns out to be one with a combination of parameter signs that contradicts the signs expected from competition, we count no model as best fitting the data. This highly conservative procedure results in inclusion of only those data vectors implicating competition in their configuration.

The first method has the difficulty that if several models producing very similar curves or surfaces are considered together, they will between them divide all the regressions of that general form, leaving other models to monopolize data

TABLE 4  
Allopatric-Sympatric Comparisons, Combined

group <sup>c</sup>	model <sup>a</sup>	Number of wins <sup>b</sup> nonlinear							Number of wins 3-parameter linear
		1	2	3	4	5	6	7	
<i>grahami</i> , large, large, HDU		1			1	1		1	1
<i>grahami</i> , small, small, HDL					2	1		2	1
<i>sagrei</i> , large, large, HDU		1	2	14	5			1	5
<i>sagrei</i> , small, small, HDU		3	1	11	10	2	15		10
<i>carolinensis</i> , large, large, HDU						2		4	
<i>carolinensis</i> , small, small, HDU					1		2	2	
<i>grahami</i> , large, large, HL				2	2	3	1	1	4
<i>grahami</i> , small, small, HU					3	3		8	1
<i>sagrei</i> , large, large, HL				3	19	6	1	3	4
<i>sagrei</i> , small, small, HL				8	8	3		29	5
<i>carolinensis</i> , large, large, HL				1		1	1	2	1
<i>carolinensis</i> , small, small, HL		1			2			4	
<i>grahami</i> , small, large, HDU		1	1			2		9	2
<i>sagrei</i> , small, large, HDU		1	10	5	19	9	2	17	17
<i>carolinensis</i> , large, combined, HDU					1	2		3	1
<i>sagrei</i> , combined, combined, HDU			2		7	3		3	4
<i>carolinensis</i> , combined, combined, HU					1			2	
Total (without linear)		1	19	23	91	51	9	101	
Total (with linear)		0	11	16	76	36	5	79	56

<sup>a</sup> Numbers refer to Table 1.

<sup>b</sup> Not including linear. Ties count as wins.

<sup>c</sup> Species, class, competitor class, category (H = height, HD = Height-diameter, U = upper finely partitioned, L = lower finely partitioned).

having different forms. Therefore we use a second-ranking method. Consider separately every possible pair of models and count the number of cases for which each member was best (Table 5). Again if the best model gives incorrect signs, the regression is not counted. Models ranked in this way formed a perfectly nested set of results; that is, Model *A* better than Model *B* and *B* better than *C* always implies *A* better than *C*. This bolsters our confidence in the numerical analysis.

As well as giving grand totals, Table 4 itemizes results by data groups. This is because certain models are much better for certain groups than others. Because

TABLE 5  
Allopatric-Sympatric Comparison, Pairwise

Model	Model					
	7 <sup>a</sup>	4	6	3	3-L	5
7	×					
4	151-127 <sup>b</sup>	×				
6	164-95	156-112	×			
3	94-82	135-24	80-79	×		
3-L	156-120	154-121	160-106	93-76	×	
5	169-113	173-82	180-70	178-70	147-77	×

<sup>a</sup> Model number corresponds to Table 1.

<sup>b</sup> Top-bottom.

the data within (and to a lesser extent between) each group are not independent, this result is not surprising. The complex, but far from complete, dependence of the data also invalidates statistical evaluation by standard techniques, such as chi-squared tests, of best model. Therefore no such evaluation is attempted.

i. *Linear vs Nonlinear Models.* In general, linear models fit less well than nonlinear models. This is despite the fact that the linear regression guarantees a global minimum SSQR, whereas the nonlinear regression does not. For all 2-parameter models combined, each of the nonlinear forms does about 1.5 times as well as the linear form; pairwise results are on the order of 1.5–2 times as well. This 2-parameter linear form corresponds to Eqs. (1), (2) or (10). Among 3-parameter models combined, the linear model does better; only the exponential and exploitative are superior. However, a 3-parameter linear model has no obvious biological interpretation because the third parameter is an intercept term tacked onto Eq. (13). This term is constant regardless of the value of  $K_h$ . The intercept, when the linear model is best, is usually positive and falls between 0.01 and 0.06. In contrast to overall results, in pairwise contests the linear model is superior only to the convex model.

As a check on the numerical analysis, comparisons can be made of the SSQR's to ensure that the 3-parameter models which are linear when  $k_3 = 0$  do at least as well as the 2-parameter linear model. Model 7 did do as well in every case, though Model 5 did not; sometimes it converged on a value for  $\rho > 1$ , even when the data were fit far better by a concave model.

When the linear model is best in the combined comparisons, its SSQR (from a sample of 37 regressions) is only 0.83 times the SSQR of the average concave nonlinear model. (Magnitudes of SSQR's mostly spanned  $10^{-1}$ – $10^{-5}$ .) When concave models are best, their SSQR's average about 0.09 times the SSQR's for

the linear model, almost an order of magnitude difference in goodness of fit. Modal ratios are 0.44 and 0.91, respectively. Thus much of the data is highly nonlinear.

ii. *Concave vs Convex Models.* Curvature in the data can be assessed in two ways. First, the concavity or convexity of  $S_S$  relative to  $S_C$  can be measured by fitting, by linear regression, the expression

$$(S_S)_h = aK_h + b(S_C)_h + c(S_C)_h^2. \quad (17)$$

This kind of expression (holding  $K$  constant) corresponds to a Taylor expansion of  $S_S$  through terms of second degree. If  $b$  and  $c$  are both negative, the data are convex; if  $b$  is negative and  $c$  is positive, the data are concave. Other combinations of signs of  $b$  and  $c$ , or cases where  $a$  is negative (almost none existed) are not counted. Of the cases with acceptable signs, 181 were concave (81 %) and 44 convex (19 %). The method does suffer from one weakness however, and that is that for certain parameter values and a concave combination of signs, the fitted function could rise above the  $S_C$  axis after dropping to some negative minimum value. In that case the connected plot for positive points would be unimodal.

A second way to examine curvature is to assess relative goodness of fit for the convex vs concave nonlinear models. This method should sometimes give different results than the Taylor Series method because for some models (e.g. the interference models from Eq. (4)), the variables are different ( $S_C/H_S$  instead of  $S_C$ ). In these comparisons if the power  $\rho$  for Model 5 gave a best fit for values less than 1, the case was not counted because then we would have another concave model. All told for acceptable combinations of signs,  $\rho$  converged to values less than 1 in 32 % of 293 cases.

For all models combined the convex was best in 21 % of 250 cases. This is very close to the 19 % figure from the first method, even though there were a substantial number of cases fit best by the Model 5 that were not fit best by the convex version of the Taylor Series. In the combined comparison (Table 4) the convex model was third best, but in pairwise comparisons the convex model did worse than all others (Table 5). Furthermore, when better, the convex model was only in terms of ratio of SSQR's 0.91 times the linear. This is in contrast to concave models.

iii. *Interference vs Exploitative Concave Models.* Considering only concave models, the best is the exploitative (101 wins), immediately followed by the exponential (91 wins). No other model is close (Table 4). When the linear model is included in the comparison, the exploitative and exponential are virtually tied (79 vs 76), since the linear model differentially robs the relatively linear exploitative. In the nested pairwise ranking of models (Table 5) the results are exploitative > exponential with refugium > interference with trade-off >

interference with refugium. Thus overall, exploitative models fit better than interference models, but the empirical exponential is also very good. Part of the reason for the latter's success may be its great degree of constancy of end result, using different starting values of the parameters. Furthermore, the interference with trade-off model, with almost the least constancy, did poorest. The exploitative however, which was not very stable, came out best nonetheless; so there is certainly no overall correlation between a model's constancy and success.

Should different kinds of lizards fit different models? We might expect that species very similar in size would show great similarity in their food resources. Such animals should undergo great exploitative competition. On the other hand animals different in size might not overlap as much in resources, but especially for the smaller member of a species pair might show relatively great effects from interference. This argument can be made precise using Eq. (8).

Where animals are similar in size, the net amount of overlapping resources ( $I_{01}$ ) is large and  $\beta \cong 1$ , so that the first term of (8) is large and a simple exploitative model (Eq. (5)) should fit relatively well.

Where animals are dissimilar in size,  $I_{01}$  should be small, but there are two possibilities for  $\beta$ :

- (1) If the competitor is *larger* than the given species, then it will eat more and perhaps appropriate resources more effectively, so that  $\beta$  should be large. Hence the first term of (8) is very small. In contrast the term involving  $\gamma_{12}$  should be very large, since smaller individuals come out much the worse in interactions. Thus (8) is very nearly

$$dN_1/dt = R_1N_1((I_{E1}/N_1) - \gamma_{12}N_2 - \gamma_{11}N_1 - C_1), \quad (18)$$

identical to Eq. (4) (Model 6), except that  $I_{E1}$  is substituted for  $I_{01} + I_{E1}$ . But since  $I_{01}$  is small, this makes little difference. Algebraically, one can show that (18) is (4) in dimensionless form to the degree that  $(I_{E1}/[I_{E1} + I_{01}])^2 = (I_{E1}/[I_{E1} + I_{01}])$ , which is nearly true for  $(I_{E1}/[I_{E1} + I_{01}])$  slightly less than one. And where  $\gamma_{12}$  is large, (18) is nearly Model 1, the other functional form for interference tested.

- (2) In contrast, if the competitor is *smaller*,  $\beta$  should be small, and since it is linearly found in the denominator of the first term in (8), (8) is nearly

$$dN_1/dt = R_1N_1[(I_{01} + I_{E1})/N_1] - \gamma_{12}N_2 - \gamma_{11}N_1 - C_1, \quad (19)$$

which is exactly (4). But  $\gamma_{12}$  is small, so this term is not as dominant as in (18).

Summarizing, we would expect similarly sized competitors to fit the exploitative model best, whereas dissimilarly sized competitors should best fit interference models. Among the latter, cases where the competitor is larger are



TABLE 6

Relationship of body-size difference to ability to be fit by interference or exploitative models.<sup>a</sup>  
Numbers in brackets are cases where competitor is smaller than or larger than test species, respectively

	Interference	Exploitative
Size of competitor similar <sup>b</sup>	32 (21-11)	52 (21-31)
Size of competitor different	57 (20-37)	37 (16-21)

<sup>a</sup> Does not include mixed runs (sets 13-17 of Table 4).

<sup>b</sup> Ratio of snout-vent lengths  $\leq 1.10$ .

especially likely to fit interference models. Data (Table 6) are entirely consistent with these expectations, though the latter effect is relatively weak.

### c. *Sympatric-Sympatric Data*

Section IV-2 gave the variables used where the given species occurred with competitors in both localities. For each model in Table 1, we can construct analogues for sympatric-sympatric comparisons. We do so here for the linear case (Eq. (13)) as an example (nonlinear analogues available upon request).

At equilibrium, we know for each  $h$

$$\begin{aligned} S_{S1} &= c_{11}(H_{S1}S_A/H_A) - c_{12}S_{C1}, \\ S_{S2} &= c_{21}(H_{S2}S_A/H_A) - c_{22}S_{C2}, \end{aligned} \quad (20)$$

where  $c_{i1} = (N_A H_S / N_S H_A)_i$  and  $c_{i2} = \alpha_{ij}(N_C / N_S)_i$ , and  $S_A$  refers to an imaginary solitary population of the widespread species. We can solve the first of (20) for  $S_A/H_A$ , substitute into the second, and define new parameters to get

$$S_{S2} = (c_1' H_{S2} S_{S1} / H_{S1}) + (c_2' H_{S2} S_{C1} / H_{S1}) - c_3' S_{C2}. \quad (21)$$

Prediction of  $S_{S2}$  is hence a three-stage instead of a two-stage linear operation: (1) Calculate the carrying capacity for Locality 2 on the basis of Locality 1; (2) add to that the loss (weighted by the habitat ratio) from the competitor of Locality 1; and (3) subtract the competitor term for Locality 2 as before. All analogues are derived by the same principle; solve in one equation for some term describing the data from an imaginary solitary-species Locality  $A$ , and then substitute this into the other to eliminate all terms for Locality  $A$ . All final equations have one more parameter than the allopatric-sympatric analogue.

For nonlinear testing, only examples with acceptable parameter signs in Eq. (21)(++-) from species that have no solitary populations were used. Each case was run twice with RAPE, first with starting parameters constant for a given model, second with parameters calculated (whenever possible) ad hoc for each case from transformations as before.

Of the nonlinear models results for the combined analysis overwhelmingly favor the exploitative model; 13 of 22 cases are best fitted by it (Table 7), with the other models evenly dividing the rest. In contrast to the allopatric-sympatric regressions however the linear model is better than any nonlinear model. However this result may be due to the increased difficulty in nonlinear regression of finding a global minimum in models with increased numbers of parameters.

TABLE 7  
Sympatric-Sympatric Comparisons

A. All models combined							
Model (#) <sup>b</sup>	Number of wins <sup>a</sup> (without linear)				Number of wins (with linear)		
Exploitative (7)	13				5		
Exponential with refugium (4)	4				2		
Interference with tradeoff (6)	4				2		
2-parameter exponential (2)	4				2		
Interference with refugium (3)	3				2		
Convex (5)	2				2		
3-parameter interference (1)	1				0		
4-parameter linear (4- <i>L</i> )	—				11		
3-parameter linear (3- <i>L</i> )	—				—		
B. Paired comparisons: number of wins							
	4- <i>L</i>	7	6	4	3	5	
4- <i>L</i>	×						4-parameter models
7	17-15 <sup>c</sup>	×					
6	16-11	18-11	×				
4	18-6	18-7	15-6	×			
3	20-3	19-4	15-4	10-8	×		
5	23-5	27-6	19-5	14-4	13-5	×	
	3- <i>L</i>	1	3				3-parameter models
3- <i>L</i>	×						
1	18-4	×					
2	15-6	11-8	×				

<sup>a</sup> Each tie counts as a win.

<sup>b</sup> # refers to Table 1.

<sup>c</sup> Top-bottom.

Pairwise comparisons, again perfectly nested, give for 4-parameter models linear > exploitative > interference with trade-off > exponential with refugium > interference with refugium > convex. Since the first three models are the most linear in  $S_C$ , this result reinforces the first comparisons. For 3-parameter models the order is: linear > interference > exponential. Again linearity is suggested.

#### d. Multiple Competitors

Both allopatric-sympatric and sympatric-sympatric models can be extended to include the competitors by simply substituting sums of  $S_C$  terms for single ones. Making the following assumptions about the constancy of certain parameters gives a set of models with  $n + 1$  or  $n + 2$  parameters, corresponding to

TABLE 8  
Multiple-Competitor Comparisons

A. All models combined						
Model (#)	Number of wins <sup>a</sup> (without linear)				Number of wins (with linear)	
Exploitative (7)	4				4	
Exponential with refugium (4)	3				2	
Interference with refugium (3)	1				1	
Interference with tradeoff (6)	0				0	
( <i>n</i> + 1)-parameter exponential (2)	0				0	
Convex (5)	0				0	
( <i>n</i> + 1)-parameter interference (1) <sup>b</sup>	0				0	
( <i>n</i> + 2)-parameter linear	—				1	
( <i>n</i> + 1)-parameter linear	—				0	
B. Paired comparisons						
	4	7	3	6	( <i>n</i> + 2)-linear	5
4	×					
7	7-5	×				( <i>n</i> + 2)-parameter models
3	5-1	6-3	×			
6	8-1	9-4	4-0	×		
( <i>n</i> + 2)-linear	9-1	11-4	4-2	9-2	×	
5	9-1	13-0	4-1	11-0	6-4	×
	1	2	( <i>n</i> + 1)-linear			
1	×					( <i>n</i> + 1)-parameter models
2	4-1	×				
( <i>n</i> + 1)-linear	5-0	5-0	×			

<sup>a</sup> Each tie counts as a win.

<sup>b</sup>  $n$  = number of competitors.

the 2- or 3-parameter models of Table 1. For the models with refugia assume that the size of the refugium is a constant fraction of the carrying capacity; this implies that the refugium is effective against the whole set of competitors. For the exploitative model assume that the exclusive resources in units of individuals is a constant fraction of the carrying capacity; this implies that resources exclusive to one competitor are exclusive to all and that the overlapping resources are divided among all competitors. For the convex model assume that  $\rho$  is the same for all competitors. In all models each competitor has a unique competition parameter associated with it. This restraint seems the most reasonable. It enhances solvability and prevents the number of parameters in the nonlinear models from escalating well above that number for the linear case.

Sixteen allopatric-sympatric cases with appropriate signs in the linear model were selected for nonlinear analysis. All these cases had only two competitors; it was very unusual to find linear regressions with more than two competitors for which all fitted competition coefficients were negative. Multiple sympatric-sympatric cases produce an enormous number of parameters and were not used.

Numerical analysis followed exactly that for sympatric-sympatric, single-competitor cases. Considering nonlinear models alone, only 8 of the 16 cases were fit best by models all of whose parameters had sensible signs. Otherwise, results are very similar to those for simple models (Table 8).

## V. CONCLUSION

In conclusion and in partial reiteration this study has the following implications.

1. Simple models alternative to those of Lotka and Volterra (L-V) have been derived from lower-level assumptions to describe interspecific competition. These models can have nonlinear but monotonic isoclines. Their derivation when compared to literal derivations of L-V suggest how different competitive mechanisms can underlie different mathematical forms. One alternative model provides a straightforward representation of the "included niche." Another with both isoclines asymptotic to nonzero axes represents more directly than L-V species with partly nonoverlapping resources. In this model extinction is deterministically impossible, though of course could exist in a stochastic version. Then extinction is likely only when the equilibrium is close to one of the axes, in contrast to the saddle of the Lotka-Volterra models. Hence distributions of extinction trajectories in the new models can be quite different.

Despite their variety, the new models display several kinds of robustness. First, several sets of assumptions can often give rise to the same isocline. This is reassuring to those needing linearity or other assumptions only at equilibrium. More importantly, over a range of models, the commonest deviation from a linear

isocline is one that is concave. Hence even if particular assumptions about competitive mechanisms are in doubt, an assumption of concavity may not be too dangerous. Interestingly, Miller (1964b) found in *Drosophila* concave per capita effects of one species on a competing species' relative abundance. Here competition apparently acts by reducing fecundity and egg viability.

2. The regression method for computing competition parameters is quite different from "overlap" methods, such as those of Levins (1966), MacArthur (1968) and Schoener (1974). Since the differences derive from different and not totally outrageous assumptions, the methods should be complementary in application.

3. The way this analysis applies the simple competition models to habitat shift is not ideal. Nonetheless, the models qualitatively parallel the data and indeed often give excellent quantitative fits (Table 9): a fairly large number of  $R^2$ 's lie between 0.9–1.0, though the rather high ratio of parameters to category number (2–3 to 7–11) diminishes the impressiveness of this result. Even for the poorer fits, the large number of cases analyzed should allow the dominant form to emerge, albeit indistinctly. Use of models with theoretically respectable origins can be contrasted with descriptive linear or "curvilinear" regression. Such analyses sometimes use quite arbitrary equations to argue (wrongly) that certain independent variables are unimportant. Nonlinear routines, while plagued by local minima, are becoming more accessible and statistically reliable as well, so that any explicit function can be tested.

TABLE 9  
Coefficients of Determination ( $R^2$ ) for Fit with Best Model<sup>a,b</sup>

Coefficient of Determination	<.61	.61-.70	.71-.80	.81-.85	.86-.90	.91-.95	.96-1.00
3-parameter models N = 11	21.3	9.7	12.3	14.8	15.5	13.5	12.9
3-parameter models N = 7	9.1	2.7	5.5	3.6	6.4	10.9	61.8
2-parameter models N = 11	17.9	11.3	15.2	17.2	17.9	11.9	8.6
2-parameter models N = 7	11.6	1.9	2.9	6.8	12.7	9.7	54.4

<sup>a</sup> Only cases where best fit has appropriate sign used.

<sup>b</sup> Rows give percent.

4. Competition seems to act concavely in cases of lizard habitat shift; that is, the per capita effect of a competitor on the abundance of a given species decreases as the competitor's abundance increases. That result is important to the field biologist trying to surmise from limited abundance data whether species compete; if competition is concave, a large range of values exist for the competing species' abundance over which the given species changes its abundance only slightly. Another way of putting this is that rare species should show little population change from place to place while common species change greatly.

The mechanism causing the isoclines to be concave is that as competing species reduce the given species' population to a low level, per capita intake of the exclusive resources increases disproportionately. Therefore in habitats crowded with competitors this greater food intake more than compensates for the competitors' deleterious effects. However another explanation is possible for the data's concavity. Sparsely used habitats may be those that would support no or few individuals of the given species. However they have more simply because they are traversed by animals going from one favorable habitat to the next. Since we have no model for the latter possibility, the two explanations have not been discriminated; the data are, as far as known, consistent with either one.

5. The analysis of habitat shift in *Anolis* is incomplete. Parameters have been calculated indirectly by fitting equations to data, but nothing has been done with them. The ability of a model to fit data, while encouraging, does not constitute anything like a complete proof that the underlying processes are those simulated in the model (Sokol, 1957). Ideally the next step would be to measure the same parameters directly and then compare the estimates. Studies of this kind are now underway.

## APPENDIX 1

While feeding, the relative frequency of Item  $k^*$  from the overlapping items in the diet of an individual of Species 2 is

$$\frac{\text{\# of item } k^* \text{ eaten per individual of Species 2/time}}{\left[ \frac{\text{\# of all overlapping items eaten}}{\text{per individual of Species 2}} + \frac{\text{\# of all exclusive items eaten}}{\text{per individual of Species 2}} \right] / \text{time}}$$

$$= \frac{\beta S p_{k^*} (\hat{N}_1 + \beta N_2)}{\frac{\beta S}{\hat{N}_1 + \beta N_2} \sum_k p_k + \frac{S}{N_2} \sum_k p_k} = \frac{\beta N_2 p_{k^*}}{\beta N_2 \sum_k p_k + \hat{N}_1 \sum_k p_k}, \quad (A1)$$

where  $S$  is the total number of items available per unit time,  $S_0$  is the number of kinds of items eaten by both species,  $S_{Ei}$  is the number of kinds of items eaten by Species  $i$  only, and  $S_i$  is the total number of kinds of items eaten by Species  $i$ ;  $S_i = S_0 + S_{Ei}$ . (The symbol over the “ $\sum$ ” refers to the set of items over which  $k$  is being summed.) Similarly the relative frequency of an exclusive item  $k^{**}$  is as (A1) but with  $p_{k^{**}}(\hat{N}_1 + \beta N_2)$  for the numerator. Then

$$A_2 = \left( \sum_k^{S_0} \beta N_2 p_k b_{2k} + \sum_k^{S_{E2}} (\hat{N}_1 + \beta N_2) p_k b_{2k} \right) / \left( \beta N_2 \sum_k^{S_2} p_k + \hat{N}_1 \sum_k^{S_{E2}} p_k \right)$$

where  $A_2$  is the average energy contributed by an item in the diet of Species 2. If an individual of Species 2 requires  $Q_2$  energy units per unit time, it will eat on the average  $n_2 = Q_2/A_2$  items. The number of items from  $S_0$  an individual of Species 2 will eat per unit time is then, using (A1),

$$n_2 \sum_k^{S_0} \frac{\beta N_2 p_k}{\beta N_2 \sum_k^{S_2} p_k + \hat{N}_1 \sum_k^{S_{E2}} p_k} = \frac{Q_2 \beta N_2 \sum_k^{S_0} p_k}{\beta N_2 \sum_k^{S_2} p_k b_{2k} + \hat{N}_1 \sum_k^{S_{E2}} p_k b_{2k}}. \quad (A2)$$

The total number of items from  $S_0$  eaten by Species 2 is (A2) times  $N_2$ . (This number can exceed the number available, so is only meaningful less than or equal to availability.) These are worth

$$J_1 = \beta N_2^2 Q_2 \sum_k^{S_0} p_k b_{1k} / \left( \beta N_2 \sum_k^{S_2} p_k b_{2k} + \hat{N}_1 \sum_k^{S_{E2}} p_k b_{2k} \right)$$

calories to Species 1. That number of calories will satisfy  $L_1 = J_1/Q_1$  individuals of Species 1 per unit time. Hence the isocline for Species 1, here convex, is  $\hat{N}_1 = K_1 - L_1$ , or text Eq. (9).

Where the convex isoclines (9) and those for (5) intersect, the terms equalling  $\hat{N}_1 - K_1$  equal each other, or

$$\frac{\beta N_2^2 c_1}{(\beta K_2 N_2 / S) + c_2 \hat{N}_1} = \frac{\beta N_2 S c_1}{\hat{N}_1 + \beta N_2}.$$

This implies

$$\hat{N}_1 = \beta N_2 (K_2 - N_2) / (N_2 - c_2 S). \quad (A3)$$

But if we solve for  $N_1$  in Eq. (9)'s analogue for  $\hat{N}_2$ , we also get (A3). Hence the concave isoclines for  $\hat{N}_1$  and  $\hat{N}_2$  intersect along the convex isocline for  $\hat{N}_1$ . By symmetry, the concave and convex isoclines for  $\hat{N}_2$  intersect along the concave isocline for  $\hat{N}_1$ . Therefore since the concave isoclines intersect in only

one place, the convex isoclines must intersect there also. And since the concave and convex isoclines both have the same intercept, there is only one intersection for each concave-convex set and therefore only one common intersection for the four isoclines.

## APPENDIX 2: TABLE OF COMMON SYMBOLS

- $A$  = total area.  
 $a$  = area.  
 $a_{ik}$  = consumption rate of an individual of Competitor  $i$  on Resource  $k$ .  
 $b_{ik}$  = net caloric value of an item of Resource  $k$  for Competitor  $i$ .  
 $C_1$  = maintenance and replacement cost of an individual of Competitor  $i$ .  
 $D_k$  = death rate of Resource  $k$ .  
 $E_1 = T_1\epsilon_1$ , where  $T_1$  is proportion of total time spent in activity and  $\epsilon_1$  is net energy harvested per unit time for an individual of Competitor 1.  
 $F_k$  = number of Resource  $k$ .  
 $f$  = fraction of  $K$  supportable on exclusive resources or by refugium.  
 $H_A$  = frequency of habitat where given species occurs alone.  
 $H_S$  = frequency of habitat where given species occur sympatrically with competitors.  
 $I_1$  = rate of net energy input into population of Competitor 1.  
 $I_{E1}$  = rate of net energy input into population of Competitor 1 of resources exclusive to that consumer.  
 $I_{01}$  = rate of energy input into system usable by both competitors, in units of net energy for Competitor 1.  
 $K_1$  = carrying capacity of Competitor 1.  
 $K_k$  = carrying capacity of Resource  $k$ .  
 $k$  = parameter to be fitted in models of Table 1.  
 $M_1$  = energy available to an individual for reproduction beyond replacement per unit time.  
 $N$  = number of individuals.  
 $p_{ih}$  = frequency of utilization of Resource  $h$  by Competitor  $i$ .  
 $p_k$  = environmental availability of Resource  $k$ .  
 $Q_1$  = energy required by an individual of Species 1 per unit time.  
 $R_1$  = number of individuals resulting from conversion of one unit net energy input for Competitor 1.  
 $r_k$  = "intrinsic rate of increase" of Resource  $k$ .  
 $S_A$  = frequency of given species where it occurs allopatrically.  
 $S_C$  = frequency of competing species.  
 $S_k$  = net rate of flow of Resource  $k$  into system.  
 $S_S$  = frequency of given species where it occurs sympatrically with competitors.



- $\alpha_{ij}$  = competition coefficient (effect of  $j$  on  $i$ ) in Lotka-Volterra system.  
 $\beta$  = likelihood of an individual of Competitor 2 getting an item relative to an individual of Competitor 1.  
 $\gamma_{12}$  = energy cost of interaction for an individual of Competitor 1 with an individual of Competitor 2 per unit time.  
 $\lambda_{12} = A_{12}/T_1$  where  $A_{12}$  is time spent by an individual of Competitor 1 in interaction with an individual of Competitor 2 per unit time, and  $T_1$  is as for  $E_1$  above.  
 $\rho$  = power in Model 5 (Table 1).  
 $*$  = converts frequencies to absolute numbers.

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