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## Competition Between Species: Theoretical Models and Experimental Tests\*

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Experimental determinations of *Drosophila* population dynamics cannot be explained by the Lotka-Volterra model of interspecific competition. This paper presents other possible mathematical models of competition between species, and gives the results of experiments designed to test the validity of such models. Eight of the ten new models presented contain the Lotka-Volterra model as a special case. The experiments made to test the models are of two kinds. Type 1 experiments are continuous one- or two-species populations, which permit the estimation of the carrying capacity of each species and the numbers of the two species at the point of stable equilibrium. Type 2 experiments measure the change in numbers over a short time interval in populations started with many different initial densities of the two species. Type 2 experiments give information on the dynamics of the two-species system in the phase plane whose coordinates are the number of individuals of each species. The models accounting best for the results are models five and seven (Table II). Each of these two models contains one parameter more than the Lotka-Volterra model. Model five adds a nonlinear term of self-interaction ( $-\beta_i N_i^2$ ). Model seven has the form,  $dN_i/dt = r_i N_i / K_i^\theta (K_i^\theta - N_i^\theta - \alpha_{ij} N_j / K_i^{1-\theta})$ . The exponential parameter  $\theta$  removes the restriction of the logistic theory of population growth, that each individual added to the population decrease the rate of growth of the population by a constant amount. With model seven the rate of growth of a population of a single species need not have its maximum at  $K/2$ , that is when the number of individuals is half the carrying capacity of the environment.

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## 1. INTRODUCTION

Lotka (1924) and Volterra (1931) proposed independently a now widely used model of interspecies competition:

$$dN_i/dt = (r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j), \quad i \neq j \quad (1)$$

where  $N_i$  is the number of individuals of species  $i$  ( $S_i$ ) at time  $t$ ,  $r_i$  is the innate capacity of increase per individual of the organisms of species  $i$ ,  $\alpha_{ij}$  is the coefficient of competition of an individual of species  $j$  on an individual of species  $i$ , and  $K_i$  is the carrying capacity of the environment for  $S_i$ , that is, the number of  $S_i$  individuals that satisfies  $dN_i/dt = 0$ ,  $r_i$ ,  $N_i > 0$ , when no individuals of other competing species are present.

The Lotka-Volterra model is based on the logistic theory of population growth and is subject to the same serious criticisms as the logistic theory since it does not take into account the age of organisms, their sex, nor genetic differences between them. It also ignores time lags and assumes that competitive interactions, both intra- and interspecific, are linear.

Despite these limitations, the model is widely used. It does give a fair representation of competition between protozoan species (Gause, 1934; Slobodkin, 1961; Vandermeer, 1969). And MacArthur (1970) has argued that the model is always applicable near an equilibrium point. Yet these considerations do not explain why the Lotka-Volterra model should be almost the only model of competition, when, for predation, there are a host of alternative models (Royama, 1971; Rosenzweig, 1971). Perhaps the reason for this state of affairs is that with competition models there are always one or more stable equilibrium points (including the axial points where only one species exists); and as parameter values are changed in a continuous fashion, the location of the stable equilibrium point(s) shifts also in a continuous fashion. With predation, however, fundamentally different outcomes are possible: a stable steady state, extinction of one or both of the populations, Lotka-Volterra oscillations, or stable limit cycles. By changing the parameters in a continuous fashion, it is possible to produce a discontinuous change in the outcome of a predator-prey system.

Because all competition models must have the same kind of behavior, i.e., convergence to a stable equilibrium point, it is difficult to distinguish between alternative models. When two species compete for the same limiting resources in a closed system, one is often at a definite advantage; the other species is then eliminated fairly rapidly. Under such conditions it is virtually impossible to test the Lotka-Volterra model against any other model, for only a few points may be obtained, and the experimental error is often large. Thus the parameters of the Lotka-Volterra model may always be fitted to the data within the experimental accuracy.

It is possible, however, to test the validity of the Lotka-Volterra model by working with experimental systems where the competing species coexist at an equilibrium. One may deduce relationships that must exist between the parameters of the Lotka-Volterra model for a stable coexistence. Obviously, if two species are to coexist, each species must be able to increase its population density when it is rare (MacArthur, 1972). By assuming that when one species is rare the other will be at a density no greater than its carrying capacity, it is possible to derive from Eqs. (1) the following inequalities that are necessary and sufficient for coexistence (cf. Gause and Witt 1935; Ayala 1970):

$$\alpha_{12} < K_1/K_2, \quad \alpha_{21} < K_2/K_1. \quad (2)$$

From these the following necessary condition may be obtained

$$\alpha_{12}\alpha_{21} < 1. \quad (3)$$

It is also possible to derive a second necessary condition, one that has a graphical interpretation. On the phase plane of a two species competitive system, the equilibrium must occur above the straight line connecting the two carrying capacities, that is, the phase plane points  $(K_1, 0)$  and  $(0, K_2)$ . That is, according to the Lotka-Volterra model, a stable equilibrium can only occur if the competition is only "conditional" (Ayala 1972).

This experimental approach was followed by Ayala (1969), who worked with two species of *Drosophila*. He showed that a stable coexistence of *D. pseudoobscura* and *D. serrata* occurs without satisfying the conditions listed above. Since then, we have conducted experiments with different strains of several pairs of *Drosophila* species. The results are summarized in Table I. In all these eight combinations a stable equilibrium occurs, yet the necessary condition  $\alpha_{12}\alpha_{21} < 1$  is false in seven cases.

In Fig. 1, the phase planes of the same eight cases are shown. Again, in seven of the eight cases, the necessary condition that the equilibrium point lie above the straight line connecting the carrying capacities is false. That is, in seven out of eight combinations, the competition is "unconditional" and yet a stable equilibrium occurs. It should be noted that five of the eight combinations of two species were replicated several times. Thus, these experiments show that the Lotka-Volterra equations are invalid for *Drosophila* competition, and, therefore, that those equations lack generality. These experiments do not, however, suggest different and perhaps more general models of competition.

An experimental approach to obtain more information about the dynamics of the competition consists in estimating the response of the competitive system. That is, to measure the  $dN_i/dt$  at various different combinations of  $N_i$  and  $N_j$ . With sufficient replication and wise selection of the initial  $N_i$ ,  $N_j$  points, a fair

TABLE I  
 Summary of Previous Experimental Studies of Interspecific Competition with *Drosophila*  
 (Means with their standard errors are given.  $n$  is the number of replicate experiments)

Code	Species	Temperature(°C)		Two-species populations		Single-species populations		$\alpha_{12} \cdot \alpha_{21}^a$	Reference
		$n$	$\bar{N} \pm \text{S.E.}$	$n$	$\bar{K} \pm \text{S.E.}$				
1	<i>D. pseudoobscura</i> AR	6	252 ± 17	3	664 ± 17	5.75	Ayala, 1969		
	<i>D. serrata</i>		278 ± 13	6	1251 ± 33				
2	<i>D. pseudoobscura</i> CH	5	132 ± 13	3	603 ± 32	4.58	Ayala, 1969		
	<i>D. serrata</i>		549 ± 26	6	1251 ± 33				
3	<i>D. pseudoobscura</i> AR + CH	6	274 ± 20	3	698 ± 19	5.17	Ayala, unpublished		
	<i>D. serrata</i>		288 ± 16	6	1251 ± 33				
4	<i>D. pseudoobscura</i>	1	511 ± 32	1	874 ± 39	2.05	Ayala, unpublished		
	<i>D. melanogaster</i> A5		491 ± 41	1	1905 ± 61				
5	<i>D. nebulosa</i>	1	679 ± 23	6	1607 ± 58	33.4	Ayala, 1972		
	<i>D. serrata</i>		75 ± 10	6	1909 ± 79				
6	<i>D. nebulosa</i>	1	308 ± 22	6	1607 ± 58	23.5	Ayala, 1970 and unpublished		
	<i>D. serrata</i>		290 ± 15	6	1909 ± 79				
7	<i>D. pseudoobscura</i>	3	399 ± 11	3	772 ± 20	1.09	Ayala, 1972 and this paper		
	<i>D. willistoni</i> M11		657 ± 18	3	1421 ± 32				
8	<i>D. pseudoobscura</i>	3	581 ± 33	3	772 ± 20	0.41 <sup>b</sup>	Ayala, unpublished		
	<i>D. willistoni</i> RP3		574 ± 40	3	1284 ± 37				

<sup>a</sup>  $\alpha_{12} = (K_1 - \bar{N}_1)/\bar{N}_2$ ;  $\alpha_{21} = (K_2 - \bar{N}_2)/\bar{N}_1$  (Ayala, 1969).

<sup>b</sup>  $\alpha_{12} = 0.33 < K_1/K_2 = 0.60$ ;  $\alpha_{21} = 1.22 < K_2/K_1 = 1.66$ .

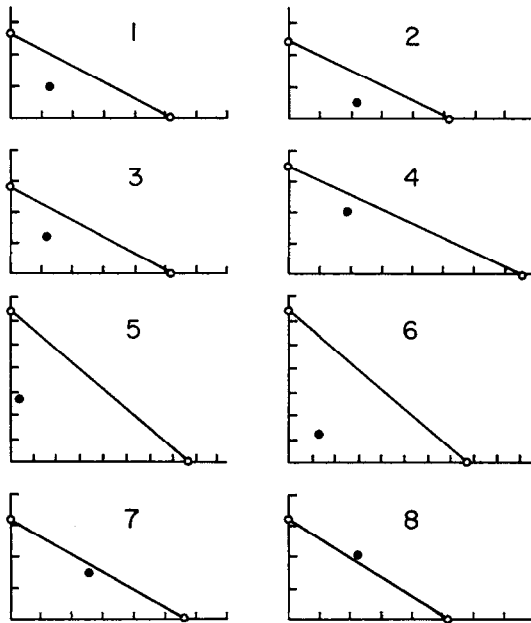


FIG. 1. Carrying capacities (open circles) and stable two-species equilibrium points (closed circles) for eight combinations of two species of *Drosophila*. The numbers 1 to 8 refer to the code numbers in Table I. In each case the numbers of the first species listed in Table I are given along the ordinate; those of the second species along the abscissa. Each division along the coordinates corresponds to 250 flies. In all cases but the last one, the point of stable two-species equilibrium falls below the straight line joining the carrying capacities.

estimation of the functional nature of the dynamic response of the system may be experimentally obtained. Since it is not experimentally feasible to divide time into infinitesimally small units, Eq. (1) may be alternatively put:

$$N_i(t + \Delta t) = N_i(t) + \Delta t(r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j) \quad (4)$$

Similarly, any other models given in the form of differential equations can be transformed into difference equations, and tested against the experimental measurements.

This method was used by Ayala (1971), who found that for a particular total density ( $N_i + N_j$ ) the competitive fitnesses of the two competing *Drosophila* species were inversely related to their relative frequency. Gilpin and Justice (1972) used the same data to produce a phenomenological model of *Drosophila* competition. Since then we have used the same method, varying both frequency and total density, to obtain a more complete description of the dynamic response

of a *Drosophila* system. These data have been used to test a variety of models of competition that have greater generality than the Lotka–Volterra model.

## 2. THE MODELS

A theoretical model is an intellectual construct purporting to describe some general phenomenon of nature. A mathematical model contains a set of parameters and state variables mutually interrelated by more or less precisely specified functions. Levins (1966) has pointed out that ideally a model should maximize generality, realism and precision. It is often not possible to maximize simultaneously those three properties of a model, but the usefulness of a model depends on how nearly it maximizes them. We believe that the usefulness of a model depends also on its simplicity—it should contain as few parameters as possible and yet describe the essential aspects of the reality under consideration. Our requirement of simplicity implies that all parameters in the model should be sufficient in Levins' sense. An additional requirement of a biological model is that the parameters of the model should have a reasonable biological interpretation. The Lotka–Volterra model of interspecific competition has been shown to be appropriate to describe the competition between certain organisms (see above). We then require, as a final restriction, that an acceptable model of interspecific competition should preferably reduce to the Lotka–Volterra model as a special case.

A competition model is a set of differential or difference equations whose solution gives the time trajectory of the state of the system. Such a model has the following general functional form:

$$dN_i/dt = D_i[N_i(t), N_j(t); r_i, K_i, \alpha_{ij}, \beta_{ij}, \dots] \quad (5)$$

where  $D_i$  is an unspecified function giving the population change per unit time,  $N_i$  and  $N_j$ , are respectively the numbers of species  $i$  and  $j$  at time  $t$ , and  $r_i$ ,  $K_i$ ,  $\alpha_{ij}$ ,  $\beta_{ij}$ , etc., are certain parameters whose values are independent of time. We assume that some essential environmental resource is limiting, that is, that the species cannot grow indefinitely. The competition function must then contain at least three such time-independent parameters, since it takes two parameters to model single species population growth when the environment has a limited carrying capacity, and a third is necessary to account for the competition. The Lotka–Volterra model is the simplest model of interspecific competition, as it is a linear three-parameter model.

Table II presents eleven models which we have chosen for various reasons and thought worth testing experimentally. There are three models with three parameters each, four models with four parameters, an additional three models

TABLE II  
Eleven Models of Interspecific Competition

Model number	Function	Number of parameters
1	$(r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j)$	3
2	$(r_i N_i / \log(K_i))(\log(K_i) - \log(N_i) - \alpha_{ij} \log(N_j))$	3
3	$(r_i N_i / K_i^{1/2})(K_i^{1/2} - N_i^{1/2} - \alpha_{ij} N_j / K_i^{1/2})$	3
4	$(r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j - \beta_{ij} N_i N_j)$	4
5	$(r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j - \beta_i N_i^2)$	4
6	$(r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j - \beta_j N_j^2)$	4
7	$(r_i N_i / K_i^{\theta_i})(K_i^{\theta_i} - N_i^{\theta_i} - \alpha_{ij} N_j / K_i^{1-\theta_i})$	4
8	$(r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j - \beta_i(1 - e^{-\gamma_i N_i}))$	5
9	$(r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j - \beta_j(1 - e^{-\gamma_j N_j}))$	5
10	$(r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j - \beta_{ij} N_i N_j - \delta_i N_i^2)$	5
11	$(r_i N_i / K_i)(K_i - N_i - \alpha_{ij} N_j - \beta_{ij} N_i N_j - \delta_i N_i^2 - \gamma_j N_j^2)$	6

with five parameters, and one model with six parameters. The first model in Table II is the Lotka–Volterra model of interspecific competition. Models four to eleven contain the Lotka–Volterra model as a special case. A variety of models besides those in Table II were also tested, most of them being extensions and recombinations of the eleven listed. They have not been included in the table because they gave no better fit than similar models with fewer parameters. The biological interpretation of the parameters in our models will be discussed below. Table III summarizes some relevant properties of the models given in Table II.

### 3. EXPERIMENTAL TESTS

To test our models we have used the two types of experiments described above. *Type 1* experiments consist of populations which are started under specified conditions, and allowed to follow their own course for many generations. We have chosen two *Drosophila* species and a set of environmental conditions which permit stable competitive coexistence between them. *Type 1* experiments started with single species provide estimates of  $K_1$  and  $K_2$ . Populations started with two species estimate the values,  $\bar{N}_1$  and  $\bar{N}_2$ , at which a stable equilibrium between the two species occurs.



TABLE III  
Analysis of the Eleven Models of Interspecific Competition

Model number	Is the Lotka-Volterra model a special case of this model?	Can the model be fitted with linear regression techniques?	Do all the terms of the model have biological significance?
1	Yes	Yes	Yes
2	No	Yes	Yes
3	No	Yes	Yes
4	Yes	Yes	Yes
5	Yes	Yes	Yes
6	Yes	Yes	Yes
7	Yes	No	Yes
8	Yes	No	No
9	Yes	No	No
10	Yes	Yes	Yes
11	Yes	Yes	Yes

Type 2 are short-time experiments. Flies of the two species are placed together at variable densities. The change in numbers after a fixed time interval estimates the vector describing the dynamics of the system at the initial densities. In the plane defined by coordinates which represent the numbers of each species, experiments of Type 2 permit a division of the first quadrant into four areas according to whether the growth of one or the other species, both species or none is positive.

The two species used in our experiments are *Drosophila pseudoobscura*, strain 211 and *D. willistoni* strain M11 (Mourão and Ayala, 1971). All experiments were conducted at 21.5°C, in half-pint (0.24 liter) milk bottles, with 30 cc of standard Spassky's medium as food. For Type 1 experiments we use the "serial transfer" technique (Ayala 1965). Adult flies are introduced into a culture bottle with food; egg laying is allowed for seven days, then the surviving adults are counted under anesthesia and transferred to a fresh culture bottle for another seven days. The process is repeated every seven days. When adult flies begin to emerge in the cultures where eggs were laid, they are collected and counted under anesthesia, and then added to the culture with the adult population. The newly emerged flies are collected and counted on the same day in which the surviving flies in the adult population are counted and transferred to a fresh culture. The cultures are discarded five weeks after the adult

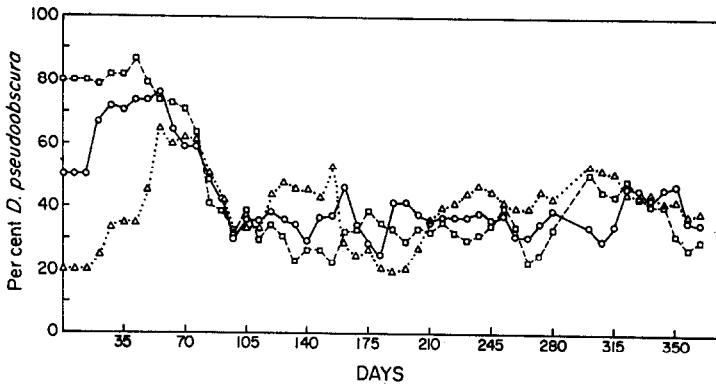


FIG. 2. Percent frequency of *Drosophila pseudoobscura* in competition with *D. willistoni* in three populations (Type 1 experiments) started with different frequencies.

TABLE IV

Mean Numbers of Flies and Standard Errors in Three "Type 1" Competition Populations (Means are calculated for measurements from day 70 to 364)

Species	Initial densities	Survivorship	Recruitment	Population size
<i>D. willistoni</i>	200	372 ± 17	318 ± 17	690 ± 30
<i>D. pseudoobscura</i>	800	265 ± 16	115 ± 10	380 ± 18
<i>D. willistoni</i>	500	361 ± 19	311 ± 20	672 ± 33
<i>D. pseudoobscura</i>	500	284 ± 17	126 ± 10	410 ± 18
<i>D. willistoni</i>	800	347 ± 20	260 ± 14	608 ± 31
<i>D. pseudoobscura</i>	200	277 ± 16	130 ± 12	407 ± 19
<i>D. willistoni</i>	Mean	360 ± 11	297 ± 10	657 ± 18
<i>D. pseudoobscura</i>		275 ± 9	123 ± 6	399 ± 11

flies are first introduced. A population consists, then, of five cultures. One culture bottle contains the ovipositing flies, whereas the four other bottles contain eggs, larvae, pupae, and newly emerged adults. The parameters measured are: the number of flies surviving after one week in the culture containing the adult flies ("survivorship"), and the number of flies emerging per week ("recruitment"). The sum of the number of flies surviving from the previous week plus the number that has emerged during the week ("total") constitutes the initial

number for the new week. The "total" number is what is considered the size of the population.

Nine populations of Type 1 were established. Three were "competition" populations. They were started with a total of 1,000 flies. The initial frequency of *D. pseudoobscura* was 20% in one population, 50% in a second, and 80% in a third. The other species was *D. willistoni*. The populations were studied for one year, or about 15 generations. The frequency of *D. pseudoobscura* among the total number of flies is shown in Fig. 2. It is clear that competitive fitness is frequency-dependent. *D. pseudoobscura* rapidly increases in frequency in the populations where its initial frequency is 20%, but decreases where its initial frequency is 80%. The frequencies of *D. pseudoobscura* rapidly converge. From about day 90 until the end of the experiment, the frequency of *D. pseudoobscura* oscillates around a mean value of about 38%. The mean numbers of flies in each of the three populations and their averages are given in Table IV. The three populations can be treated as replicates since they are not significantly heterogeneous.

TABLE V

Mean Numbers of Flies and Standard Errors in Three "Type-1" Single-Species Populations (Means are calculated for measurements from day 70 to 364)

Species	Initial density	Survivorship	Recruitment	Population size
<i>D. willistoni</i>	200	903 ± 25	587 ± 31	1490 ± 54
<i>D. willistoni</i>	500	881 ± 31	576 ± 28	1457 ± 48
<i>D. willistoni</i>	800	790 ± 39	527 ± 25	1317 ± 59
<i>D. willistoni</i>	Mean	858 ± 21	564 ± 16	1421 ± 32
<i>D. pseudoobscura</i>	200	607 ± 27	169 ± 14	776 ± 35
<i>D. pseudoobscura</i>	500	616 ± 31	163 ± 13	779 ± 38
<i>D. pseudoobscura</i>	800	598 ± 26	163 ± 13	761 ± 34
<i>D. pseudoobscura</i>	Mean	607 ± 16	165 ± 8	772 ± 20

Three Type 1 populations were established with *D. pseudoobscura* and three others with *D. willistoni*. In each set, one population was started with 200 flies, another with 500, and a third with 800 flies. Within each set the numbers of flies in the three populations converge rapidly. The mean numbers of flies for each population and the averages for each species are given in Table V.

Type 2 experiments are conducted as follows. Adult flies in given densities are placed in a culture with medium as above. After seven days the survivors are counted and discarded. The flies emerging from that bottle until the end

TABLE VI

"Type 2" Experiments of 1969-1970 (Mean numbers of flies and standard error for survivorship, recruitment, and total, at various initial densities of two species of *Drosophila*.  $n$  is the number of replications)

Species	Initial number	$n$	Survivors after one week	Recruitment	Total
<i>D. willistoni</i>	200	54	101 ± 4	168 ± 10	287 ± 3
<i>D. pseudoobscura</i>	800		563 ± 11	164 ± 15	727 ± 8
<i>D. willistoni</i>	500	52	277 ± 8	315 ± 19	592 ± 2
<i>D. pseudoobscura</i>	500		359 ± 8	183 ± 14	541 ± 9
<i>D. willistoni</i>	800	54	465 ± 14	501 ± 23	966 ± 41
<i>D. pseudoobscura</i>	200		152 ± 2	168 ± 11	320 ± 8
<i>D. willistoni</i>	200	24	154 ± 5	491 ± 25	645 ± 25
<i>D. pseudoobscura</i>	0		—	—	—
<i>D. willistoni</i>	500	24	363 ± 14	725 ± 38	1088 ± 39
<i>D. pseudoobscura</i>	0		—	—	—
<i>D. willistoni</i>	800	24	547 ± 26	728 ± 55	1276 ± 59
<i>D. pseudoobscura</i>	0		—	—	—
<i>D. willistoni</i>	1000	20	650 ± 26	768 ± 28	1419 ± 38
<i>D. pseudoobscura</i>	0		—	—	—
<i>D. willistoni</i>	0	24	—	—	—
<i>D. pseudoobscura</i>	200		161 ± 4	306 ± 21	467 ± 20
<i>D. willistoni</i>	0	24	—	—	—
<i>D. pseudoobscura</i>	500		397 ± 7	260 ± 22	656 ± 23
<i>D. willistoni</i>	0	24	—	—	—
<i>D. pseudoobscura</i>	800		606 ± 16	231 ± 24	837 ± 28
<i>D. willistoni</i>	0	20	—	—	—
<i>D. pseudoobscura</i>	1000		759 ± 20	172 ± 18	931 ± 27

of week five are also counted. The sum of the number of survivors plus the number of flies emerging from the bottle estimates the total number of flies after one week in populations of Type 1 which at a certain point in time would have the initial densities of the Type 2 populations. In other words, we are estimating  $dN_i/dt$  for a period of one week, at given initial values of  $N_1$  and  $N_2$ . It should be pointed out that the flies used for each Type 2 experiment were developed in cultures where the two species competed at precisely the densities used in the experiment.

TABLE VII

"Type 2" Experiments of 1970-1971 (Mean numbers of flies and standard errors for survivorship, recruitment, and total, at various initial densities of two species of *Drosophila*. *n* is the number of replications)

Species	Initial number	<i>n</i>	Survivors after one week	Recruitment	Total
<i>D. willistoni</i>	100	15	34 ± 2	35 ± 7	68 ± 7
<i>D. pseudoobscura</i>	1400		777 ± 28	153 ± 10	930 ± 28
<i>D. willistoni</i>	200	15	116 ± 5	172 ± 21	287 ± 21
<i>D. pseudoobscura</i>	400		294 ± 7	252 ± 14	545 ± 14
<i>D. willistoni</i>	200	20	104 ± 6	136 ± 19	240 ± 21
<i>D. pseudoobscura</i>	600		404 ± 15	135 ± 15	539 ± 25
<i>D. willistoni</i>	200	20	94 ± 6	122 ± 21	216 ± 24
<i>D. pseudoobscura</i>	1000		636 ± 36	107 ± 11	743 ± 24
<i>D. willistoni</i>	200	15	79 ± 7	73 ± 15	151 ± 20
<i>D. pseudoobscura</i>	1200		670 ± 50	98 ± 11	768 ± 53
<i>D. willistoni</i>	200	18	60 ± 6	45 ± 12	105 ± 15
<i>D. pseudoobscura</i>	1400		644 ± 48	87 ± 10	731 ± 47
<i>D. willistoni</i>	400	15	235 ± 11	356 ± 34	591 ± 40
<i>D. pseudoobscura</i>	400		291 ± 7	157 ± 21	448 ± 24
<i>D. willistoni</i>	400	21	214 ± 12	180 ± 25	394 ± 27
<i>D. pseudoobscura</i>	600		413 ± 16	118 ± 14	531 ± 26
<i>D. willistoni</i>	400	20	196 ± 13	186 ± 26	382 ± 32
<i>D. pseudoobscura</i>	800		496 ± 21	109 ± 15	605 ± 28
<i>D. willistoni</i>	800	21	406 ± 26	241 ± 29	647 ± 41
<i>D. pseudoobscura</i>	600		369 ± 22	85 ± 10	455 ± 29
<i>D. willistoni</i>	800	14	332 ± 26	175 ± 23	507 ± 42
<i>D. pseudoobscura</i>	800		445 ± 35	82 ± 13	527 ± 43
<i>D. willistoni</i>	1200	20	741 ± 28	499 ± 26	1240 ± 40
<i>D. pseudoobscura</i>	60		44 ± 1	42 ± 5	86 ± 5
<i>D. willistoni</i>	1200	19	721 ± 39	416 ± 37	1137 ± 55
<i>D. pseudoobscura</i>	200		134 ± 6	70 ± 8	204 ± 13
<i>D. willistoni</i>	1200	20	679 ± 35	362 ± 30	1041 ± 52
<i>D. pseudoobscura</i>	400		243 ± 13	56 ± 6	298 ± 17
<i>D. willistoni</i>	1600	18	805 ± 39	340 ± 17	1145 ± 47
<i>D. pseudoobscura</i>	100		68 ± 4	68 ± 8	136 ± 8

(Table continued)

TABLE VII (continued)

Species	Initial number	<i>n</i>	Survivors after one week	Recruitment	Total
<i>D. willistoni</i>	1600	17	749 ± 28	262 ± 22	1011 ± 31
<i>D. pseudoobscura</i>	300		167 ± 7	50 ± 5	217 ± 10
<i>D. willistoni</i>	1800	15	950 ± 36	326 ± 24	1277 ± 45
<i>D. pseudoobscura</i>	100		68 ± 4	58 ± 8	126 ± 11
<i>D. willistoni</i>	2200	10	1090 ± 96	581 ± 57	1671 ± 138
<i>D. pseudoobscura</i>	100		62 ± 5	21 ± 5	83 ± 6
<i>D. willistoni</i>	2600	10	1216 ± 100	519 ± 50	1735 ± 143
<i>D. pseudoobscura</i>	100		52 ± 6	29 ± 6	81 ± 9
<i>D. willistoni</i>	1400	20	910 ± 47	556 ± 22	1466 ± 55
<i>D. pseudoobscura</i>	0		—	—	—
<i>D. willistoni</i>	1600	21	922 ± 45	434 ± 28	1356 ± 56
<i>D. pseudoobscura</i>	0		—	—	—

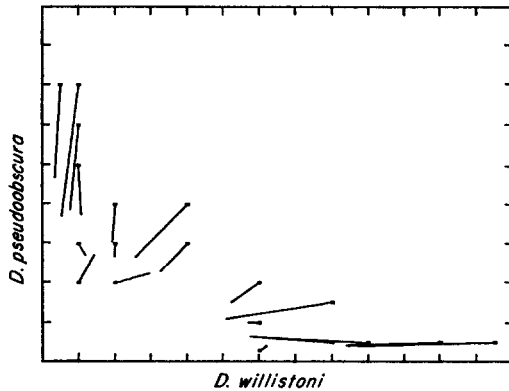


FIG. 3. Computer-drawn displacement vectors showing the change in numbers of flies from 19 different initial densities of two species, *Drosophila pseudoobscura* and *D. willistoni* (Type 2 experiments). The dots indicate the initial densities; the tip of the vector indicates the density after one week. Each division along the coordinates corresponds to 200 flies.

Type 2 experiments were conducted in two sets. The first set of experiments was conducted during 1969–1970; the second set was conducted one year later and by a different person. The results are given in Tables VI and VII. We have kept these results separately. As it will be shown later the results of both sets are not perfectly mutually consistent. We obtain a better fit of the

data to our models when the results of the second set of experiments alone are used, than when both sets are used. The results of the second set of experiments (except those in which the initial frequency of one species is zero) are graphically represented in Fig. 3. The vectors indicate the change in numbers in the phase plane.

#### 4. GRAPHICAL INVESTIGATION OF THE DATA

The per week population displacement vectors shown on the system's phase plane (Fig. 3) contain a great deal of information. The "phase plane niche" of each species may be interpolated by eye. The phase plane niche is that area of the system's phase plane in which the growth of a species is positive. Thus, for *Drosophila willistoni*, whose density is plotted along the abscissa, this is the area where the  $x$ -component of the population displacement vector is positive. For *D. pseudoobscura*, the phase plane niche is that area where the  $y$ -component of the population displacement vector is positive. The line that delimits a phase plane niche is the zero isocline for that population; on this line, the growth of that population is zero. Figure 4 shows that approximate shape of the two phase plane niches. To avoid unnecessary confusion, the population displacement vectors have been reduced to a third of their true length.

Given this figure, the carrying capacities of the two populations and their equilibrium point are determined. The carrying capacities,  $K_w$  and  $K_p$ , occur

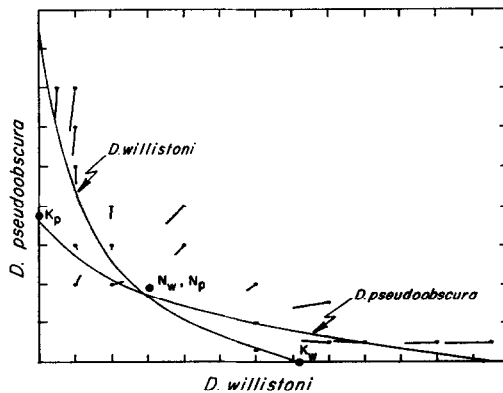


FIG. 4. Zero isoclines containing the points at which the growth of one species is zero. The length of the vectors (Type 2 experiments) has been reduced to one third of their actual length for clarity. The isoclines have been fitted by visual inspection of the vectors. Each division along the coordinates corresponds to 200 flies.  $N_w$ ,  $N_p$ , and  $K_w$  and  $K_p$  are respectively the equilibrium point and the carrying capacities as estimated by Type 1 experiments.

where a zero isocline intersects the species axis. The equilibrium point is where the two zero isoclines cross. It is obvious that this equilibrium point is stable, since the population displacement vectors in the four zones about the equilibrium all point towards the equilibrium point. That the two populations will coexist can be inferred another way. A sufficient condition for coexistence is that when a species is rare it must have a wider niche than its competitor. In a narrow strip along the abscissa in Fig. 4, *D. pseudoobscura*, which is rare, has a wider niche (it extends further) than *D. willistoni*. The converse holds along the ordinate. From the overall point of view of the competition system, this of course implies that the competitive fitnesses of the species are inversely related to their frequencies, at least in the areas near the zero isoclines.

In Fig. 4 we have also indicated the two carrying capacities  $K_w$  and  $K_p$ , and the equilibrium point  $\bar{N}_w$ ,  $\bar{N}_p$  as determined by the Type 1 experiments. The agreement between the two types of experiments is good, which substantiates that the Type 2 experiments give a good idea of the dynamics of the system. This also establishes a kind of ergodic principle for experimental population biology. That is, for genetically similar populations, a time average for a single population is equivalent to an ensemble average over sets of replicate populations.

### 5. DATA FITTING

To be able to evaluate the various competition models, each model must be fitted to the data. For a particular model, the parameters that produce an optimal fit to the data are found by minimizing the expression

$$Q_i = \sum_k \frac{1}{\sigma_{ik}^2} (D_{ik}^e - D_i(N_{ik}, N_{jk}; r_i, K_i, \alpha_{ij}, \dots))^2 \tag{6}$$

where  $D_{ik}^e$  is the  $k$ -th experimental population displacement for the  $i$ -th species, where  $\sigma_{ik}^2$  is the variance of this  $k$ -th displacement for the  $i$ -th species, and where  $D_i(N_{ik}, N_{jk}; r_i, K_i, \alpha_i, \dots)$  is the  $i$ -th competition function whose parameters are to be determined.

For models 1, 2, 3, 4, 5, 6, 10, and 11, the parameters are in a form for which linear regression techniques can be used, that is, where the minimization of  $Q_i$  follows from a matrix inversion. To allow this, the parameters are transformed to a purely linear form. For example, with model 1, the Lotka-Volterra model, the transformation is  $X_1 = r$ ,  $X_2 = r/K$ , and  $X_3 = r\alpha/K$ , which gives the linear model

$$dN_1/dt = X_1N_3 - X_2N_1^2 - X_3N_1N_2,$$

and similarly for the second species.



Models 7, 8 and 9 have parameters that occur as exponents. For these, gradient, or hill climbing, techniques must be used. There were no insurmountable difficulties with this, for each functional surface had but a single hill, to whose summit convergence was rapid.

From either fitting technique, goodness of fit can be tested with a multiple regression correlation coefficient for the whole model,  $R^2$ , which is defined as

$$R^2 = 1 - Q_i / \sum_k \frac{1}{\sigma_{ik}^2} (D_{ik}^e)^2. \quad (7)$$

Essentially, this statistic tells us how much of the experimental variance is explained by each model.

$R^2$  should be as close to unity as possible. It appeared, however, that experimental errors prevented  $R^2$  from going above about 0.95, since models with more parameters than the models given in Table II did not increase the value of  $R^2$ . For this reason, these more complex models are not listed.

Our requirement that the model has as few parameters as possible suggests an additional test of goodness of fit, namely a  $t$ -value where the significance of each parameter,  $\tau$ , can be tested ( $H_0 : \tau = 0$ ).  $t$ -values smaller than 2 are

TABLE VIII  
Statistical Analysis of Eleven Models of Interspecific Competition:  
32 Data Points

Model number	<i>Drosophila willistoni</i>			<i>Drosophila pseudoobscura</i>		
	Explained variance	Lowest $t$ -value	Least significant parameter	Explained variance	Lowest $t$ -value	Least significant parameter
1	.810	5.66	$\alpha$	.790	6.24	$\alpha$
2			could not be fitted			
3			could not be fitted			
4	.827	1.60	$\beta$	.861	3.79	$\beta$
5	.912	5.70	$\beta$	.917	6.42	$\beta$
6	.811	.052	$\beta$	.813	1.89	$\beta$
7			could not be fitted			
8	.916	1.10	$K$	.940	5.90	$K$
9	.815	1.21	$r$	.822	2.06	$r$
10	.913	0.52	$\beta$	.923	1.75	$\beta$
11	.926	2.08	$\beta$	.924	0.31	$\beta$

below the 95% significance level; thus any parameter associated with such a value cannot be deemed different from zero. If any parameter of the model is below this level, the entire model is considered unacceptable.

Table VIII shows the statistical tests for goodness of fit for the models, when all 32 data points from Type 2 experiments are used. Models 2, 3, and 7 could not be fitted; the computer programs "blew up" because of the inclusion of points with one or the other species at zero density. A second fit was made using just 19 data points, the points off the axes from the second set of Type 2 experiments. That is, excluding the displacements from the points (800, 200), (500, 500) and (200, 800), made by the other researcher, and all points with  $N_1$  or  $N_2$  equal to zero. All models could then be fitted. The results are given in Table IX. The  $R^2$  statistic is consistently higher when only these 19 points are used.

TABLE IX  
Statistical Analysis of Eleven Models of Interspecific Competition:  
19 Data Points

Model number	<i>Drosophila willistoni</i>			<i>Drosophila pseudoobscura</i>		
	Explained variance	Lowest $t$ -value	Least significant parameter	Explained variance	Lowest $t$ -value	Least significant parameter
1	.883	4.80	$r$	.840	5.71	$r$
2	.784	—	—	.823	—	—
3	.926	8.18	$r$	.917	9.68	$\alpha$
4	.898	2.07	$\beta$	.923	4.99	$\alpha$
5	.959	7.21	$\beta$	.949	7.75	$\beta$
6	.884	0.45	$\beta$	.870	2.59	$\beta$
7	.930	9.91	$r$	.953	8.94	$r$
8	.959	6.41	$K$	.960	3.45	$K$
9	.886	0.93	$\beta$	.904	3.21	$K$
10	.965	2.31	$\beta$	.950	0.81	$\beta$
11	.967	1.01	$\gamma$	.950	0.22	$\beta$

A third test of goodness of fit is possible. Once the parameters of a model are estimated, the carrying capacity of each species and the two-species equilibrium point can be calculated. These may then be compared to the mean densities in the continuous populations with one or two species. Table X gives the  $K$ 's and the equilibrium points estimated from the various models. Only the 19 data

points have been used. The goodness of fit is tested by a statistic, "Total Error" (T.E.), defined as

$$\begin{aligned} \text{T.E.} = & |K_w^{\text{obs}} - K_w^{\text{exp}}| + |K_p^{\text{obs}} - K_p^{\text{exp}}| \\ & + ((\bar{N}_w^{\text{obs}} - \bar{N}_w^{\text{exp}})^2 + (\bar{N}_p^{\text{obs}} - \bar{N}_p^{\text{exp}})^2)^{1/2}, \end{aligned} \quad (8)$$

where the  $K$ 's are the carrying capacities, the  $\bar{N}$ 's are the numbers at the two species equilibrium points, the subscripts  $p$  and  $w$  refer to the species, the superscript "obs" refers to the observed number, and the superscript "exp" to

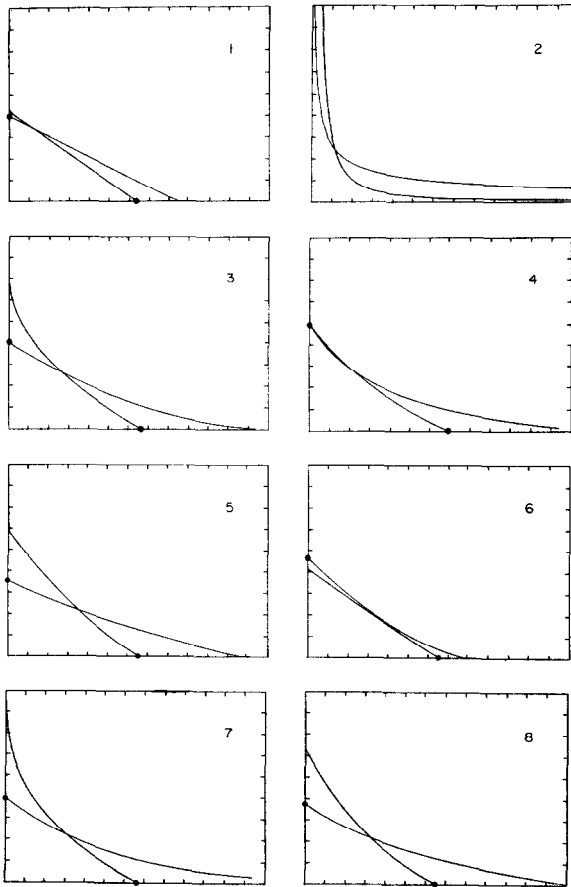


FIG. 5. Computer-drawn zero isoclines for each of the first eight models given in Table II. Abscissa: *Drosophila willistoni*; ordinate: *D. pseudoobscura*. Each division along the coordinates correspond to 200 flies. The solid circles are the carrying capacities predicted by each model.

the number predicted by the model. Finally, there is a nonquantitative measure by which the models may be evaluated. Once the parameters of a model are determined, the zero isocline which delimits the phase space niche may be drawn. In Fig. 5 this has been done for the first eight models in Table II. The zero isoclines should be similar in shape and position to those drawn by eye in Fig. 4.

TABLE X

Carrying Capacities and Equilibrium Population Densities Predicted by the Models.  
19 Data Points

Model number	<i>Drosophila willistoni</i>		<i>Drosophila pseudoobscura</i>		Total error
	Carrying capacity	Equilibrium density	Carrying capacity	Equilibrium density	
Experimental values	1421 ± 32	657 ± 18	772 ± 20	399 ± 11	
1	1277	237	800	687	681
2	13752	230	9965	480	21958
3	1334	539	806	520	290
4	1392	439	990	553	513
5	1314	708	711	434	229
6	1317	no equilibrium	934	no equilibrium	—
7	1332	616	791	441	166
8	1310	653	750	430	164
9	1488	700	1260	330	636
10	1257	770	750	408	300
11	1297	642	743	508	263

## 6. RESULTS

Tables VIII, IX and X contain the results of fitting the models to the experimental observations. In Table VIII we have used all data from the two sets of Type 2 experiments (Tables VI and VII), or a total of 32 points. In Table IX only data from the second set of Type 2 experiments (Table VII) were used, a total of 19 points (points on the axes were excluded, see above). Yet the explained variance,  $R^2$ , is lower for every model when 32 rather than 19 points are used. This indicates that the two sets of data are not mutually consistent. The two sets of experiments were carried out by two different researchers and

about one year apart. Although every effort was made to keep the techniques identical, it appears that this was not perfectly so. This is confirmed by examination of the data since the displacement vectors from the points (200, 800), (500, 500), and (800, 200) are clearly at odds with the general pattern of the other 19 points off the axes.

If we compare the models using the  $R^2$  statistic we find that the relative differences between the models are approximately the same in Table VIII as in Table IX. Moreover, if the models are ranked according to the  $R^2$  statistic, the rankings are identical for *D. pseudoobscura*, while for *D. willistoni* only the second and third ranking models are interchanged. It seems, then, preferable to ignore the results of Tables VI and VIII. The following comments are based on the results of Tables IX and X.

Model 2 fits the data very poorly. Furthermore, the shapes of the isoclines in Fig. 5 are highly implausible. It can be summarily dismissed.

The Lotka-Volterra (model 1) can explain about 86 percent of the variance, but it gives a bad prediction of the equilibrium point. Moreover, it cannot explain the obvious curvature of the zero isoclines. This model does not permit a stable equilibrium below the straight line joining the two carrying capacities, while in seven out of eight combinations of two species of *Drosophila* a stable equilibrium occurred below that line. The addition of a single parameter to this model gives a significantly better fit, accounts for the curvature of the zero isoclines and predicts well the equilibrium point.

Model 3, which is a special case of model 7, is also a three parameter model. It fits the data surprisingly well and accurately models the shape of the zero isoclines. The exponent of 1/2 appears highly artificial, although it may have some biological meaning that we have not yet recognized.

From examining models 6 and 9, which fit the data poorly, it is clear that nonlinearities in the interspecific interaction are of little or no importance. We conclude that the competitive effect of one species on the growth of another is linearly proportional to the density of the first.

Model 4 introduces a multiplicative interaction between the species. It fits the data better than models 6 and 9, which posit nonlinear competition. But it does not fit the data as well as models 5, 7, and 8, in which the nonlinearities are solely involved in single species growth. Additionally, in the inclusive models, 10 and 11, the significance of the multiplicative interaction term ( $\beta N_i N_j$ ) is low.

Model 5 adds to the Lotka-Volterra model a term,  $-\beta_i N_i^2$ , which is a nonlinear term of self-interaction. This self-interaction will be cooperative when  $\beta$  is negative, and competitive when  $\beta$  is positive. This model fits the data very well, but it has some mathematical difficulties. It predicts a parabolic zero isocline. If  $\beta$  is negative, as in our case, at sufficiently high densities, the parabola will reenter the positive quadrant of the phase plane, which implies that at

high densities the positive feedback from synergistic self-interactions will make the population grow despite the effects of intra- and interspecific competition. This feature of the model runs counter to all biological reason. An additional undesirable feature of this model is that the  $K$ 's do not represent the carrying capacities.

Model 8 fits the data also very well. Like model 5, it can account for about 95 percent of the variance. The  $R^2$  statistic for *D. willistoni* is in fact identical in the two models, and it is not very different for *D. pseudoobscura*. Despite appearances to the contrary model 8 and model 5 are very similar to each other. The reason for this is as follows. The term  $\beta_i(1 - e^{-\gamma_i N_i})$  can be expanded in a power series to give

$$\beta_i(1 - 1 + \gamma_i N_i - (\gamma_i N_i)^2/2 + \dots)$$

When this term is added to the remaining terms in model 8, this becomes (to second order)

$$r_i N_i / K_i [K_i - (1 + \beta_i \gamma_i) N_i - \alpha_{ij} N_j + \beta_i \gamma_i^2 N_i^2 / 2],$$

which has the same mathematical form as model 5. Model 8, however, does not have the unfortunate feature of predicting growth at very high densities. Yet it is less desirable than model 5 (and model 7) in that it has one more parameter. Furthermore it is not clear in model 8 what the biological meaning of some parameters may be.

Model 7 is a four parameter model which fits the data very well. It explains about 95 percent of the variance, like model 5; moreover, all parameters are highly significant. In terms of total error, model 7 is somewhat better than model 5. The prediction of the equilibrium numbers and of the carrying capacities is indeed quite accurate (the best, together with model 8). Moreover, it does not have the mathematical weaknesses of model 5, and all its terms have biological interpretation. All in all, model 7 is the best of the models considered in this paper.

Model 10 is an inclusive combination of models 4 and 5; model 11 includes also model 6. Models 10 and 11 explain slightly more than 95 percent of the variance, but they are in this respect not much better than models 5 and 7, although these contain only four parameters. Both models 10 and 11 have the same undesirable features as model 5. The prediction of the equilibrium point and carrying capacities of models 10 and 11 is not as good as that of model 5, and definitely worse than that of model 7. The terms in the parentheses of the Lotka-Volterra model can be recognized as equivalent to a first order Taylor's expansion, and were obtained in this manner by Lotka. The terms in the parentheses of model 11 are equivalent to a second order Taylor's expansion.

## 7. BIOLOGICAL SIGNIFICANCE OF THE MODELS

Model 1, the Lotka-Volterra model, is a well-known extension to interspecific competition of the logistic theory of population growth. The terms of this model enter in all the models suggested in this paper (although they do not have the same biological meaning in every model) and have obvious biological interpretation. In the Lotka-Volterra model,

$N_i$  is the number of individuals of species  $i$  ( $S_i$ ) at a given time;

$r_i$  is the innate capacity for increase per individual, which results from the difference between birth and death rates;

$K_i$  is the carrying capacity of the environment for species  $i$ , when no other species is present. The exponential rate of growth  $r_i N_i$  is decreased by a factor of  $1/K_i$  by each individual of  $S_i$ ;  $1/K_i$  measures intraspecific competition.

$\alpha_{ij}$  measures interspecific competition; the exponential rate of growth of species  $i$  is decreased by a factor of  $\alpha_{ij}/K_i$  by each individual of species  $j$ .

Model 2 has been suggested by Coleman and Gomatan (in press) and is included here for completeness. It has the interesting feature that it can be solved analytically. It can account for the curvature of the zero isoclines, but it gives the worst fit of all the models tested. We do not find any clear biological interpretation for it. The only interpretation that we can suggest is that the realized intensity of the competition increases logarithmically.

Model 3 is a special case of model 7, discussed below.

Model 4 adds to model 1 a term for multiplicative interaction between the species ( $-\beta_{ij}N_iN_j$ ). In this model, the  $\alpha$ 's can be interpreted as measuring competition due to sharing of resources, while the  $\beta$ 's would measure interactions between the individuals, either directly and/or through their effects on the environment other than use of resources. For instance, adult *Drosophila* of one species may interfere with those of the other species through collision, handicap of the egg laying process, etc. The interaction described by the  $\beta$  term can be cooperative (synergistic) if  $\beta$  is negative, or disoperative (antagonistic) if  $\beta$  is positive.

Model 5 adds also one term to the Lotka-Volterra model. This additional term ( $-\beta_i N_i^2$ ) can be interpreted to mean self-interactions among members of the same species, other than sharing of resources. The value of  $\beta$  can be either positive or negative, depending on whether the interactions are disoperative or cooperative, respectively. The  $\beta$  term could, for instance, account for harmful collisions between adult individuals, which would increase with the square of the density; and/or interference with egg laying, the effect of accumulation of catabolites, etc. Cooperative interactions could be due to conditioning of the

food medium, to decreasing the negative effects of the catabolites or behaviors of the competing species, etc. In model 4, the  $\beta$  term accounted only for interactions between individuals of *different* species, but not between individuals of the same species. The opposite is true for model 5.

Model 6 is similar to model 5, except that the second order term ( $-\beta_i N_j^2$ ) is due to interactions between individuals of the competing species,  $S_j$ . The term could represent behavior or effects of  $S_j$  other than resource sharing, which would affect the growth of  $S_i$ . The effect on  $S_i$  could be cooperative or disoperative, as above, depending on the sign of  $\beta$ .

Model 7, as pointed out above, gives the best fit to the data. It has also an attractive biological interpretation, which extends to the logistic growth of a single species as well. All parameters, except  $\theta$ , have the same interpretation as in the Lotka–Volterra model. The exponent,  $\theta$ , changes the function relating rate of growth to density. In the logistic growth that function is symmetrical around  $K/2$ ; with the use of  $\theta$ , that restriction is removed. The maximum rate of growth will be at a density smaller (greater) than  $K/2$  if  $\theta$  is smaller (larger) than one. It is well known that the rate of population growth often increases faster when density is relatively low, and reaches its maximum well below half the carrying capacity of the environment. These features can be approximated with model 7. We are planning further theoretical and experimental work to explore this model.

Model 8 incorporates the function of the law of diminishing returns as used in economics. It has some interesting mathematical properties, and gives a very good fit, although at the expense of one more parameter than models 5 and 7, which also fit the data very well. It has no obvious biological interpretation except as it reduces to model 5. Its advantage over model 5 is that model 8 establishes an upper bound for the second order interaction whose maximum value is  $\beta$  and is reached when  $N_i$  is large. Model 9 was included for completeness. As seen above, it gives a very poor fit.

Models 10 and 11 incorporate the terms of models 4, 5, and 6. Their biological interpretations can be made as suggested above. For instance, the  $\beta$ ,  $\gamma$ , and  $\delta$  terms of model 11 would represent the second order interactions between all individuals of the same or of different species.

## 8. DISCUSSION AND CONCLUSIONS

The widely used Lotka–Volterra model of competition between species cannot account for the process of competition as studied in experimental systems with *Drosophila* species. That model, then, lacks generality. We have explored other possible models that could have greater generality, and perhaps be also more precise and realistic.



If we exclude model 2, which does not seem worth further consideration, the models investigated fall into two groups. One group comprises the Lotka-Volterra model and models 4, 5, 6, 10 and 11 (and by reduction models 8 and 9) given in Table II. These models can be considered as an extension of the Lotka-Volterra model by adding to it some or all of the second order terms of a Taylor's expansion. Model 11 is the most inclusive, and could perhaps be chosen as the general model of this group. Not all the parameters in this model are necessarily significant in every case of interspecific competition. Experimental studies should permit to ascertain which ones, if any, of the terms can be dropped in each case. The Lotka-Volterra model, without any of the second order terms, has been shown to be sufficient to account for the competition process among protozoan species (Gause, 1934; Slobodkin, 1961; Vandermeer, 1969). In the present study, two of the second order terms can be dropped without loss of precision or reality.

The second group of models includes model 7 and its particular case, model 3. Model 7 has some attractive mathematical and biological features which make it worth further investigation. We hope that other investigators will test its validity with other systems, including organisms other than *Drosophila*. Our experimental method can be used with other organisms. Experiments of Type 2 provide a great deal of information with a manageable amount of work. The direction and length of displacement vectors in the phase plane of the two species can provide the crucial information to test our models or any others of the same general form. Measuring the carrying capacities for each species and the two-species point(s) of stable equilibrium, if such exist(s) provide additional tests.

It is, of course, difficult to ascertain the bearing that any of our models may have on the competition process as it occurs in nature. In the field, more than two species may often compete for the same resources, and additional complexities are likely to occur which do not exist in the laboratory. Experimentally tested models, however, may help in the understanding of natural processes.

A widely accepted notion states that two competing species can stably coexist only if their competition is *conditional*, as defined by Ayala (1972); that is, only if the point of equilibrium in the phase plane is above the diagonal joining the carrying capacities of the two species. We have shown that this requirement, although a necessary condition in the Lotka-Volterra model, is not a necessary requirement of other competition models. Experiments have shown that two-species stable equilibria can also occur below the diagonal joining the carrying capacities of the two species; that is, when the competition between the species is *unconditional*.

The Lotka-Volterra model permits no more than one equilibrium point, whether stable or unstable, since the zero isoclines are straight lines. This restriction does not occur in our models where the isoclines are curved. It is

thus possible for the zero isoclines to cross twice; one of the equilibria will then be stable, the other unstable, depending on the sign of the difference between the first derivatives of the isoclines at the points where they cross (Gilpin and Justice, 1972). Our Type 1 experiments were started at three different frequencies of the two species which nevertheless converged to the same point of stable equilibrium. Our Type 2 experiments confirm that in the *Drosophila* experimental system, there is only one point of stable equilibrium with both species present. Whether there are any points of unstable equilibrium cannot, by definition, be determined by experiments of Type 1. The evidence from our Type 2 experiments does not suggest any such points of unstable equilibrium.

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