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A SEARCH FOR EMERGENT COMPETITIVE PHENOMENA: THE DYNAMICS OF MULTISPECIES *DROSOPHILA* SYSTEMS[1]

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Abstract. Theoretical analyses of multispecies competition suggest that the stable co-existence of three competing species may occur even when all the pairwise combinations of the same species do not result in stable equilibria. In an attempt to discover such an emergent property of multispecies competition, we constructed laboratory populations consisting of one, two, and three species of *Drosophila* in all possible combinations. Two series of experiments at 19° and 22°C were conducted. We found no evidence of emergent behavior; the outcome of competition in three-species populations could be adequately predicted from a knowledge of the pairwise interactions among the species.

Key words: Competition; Drosophila; *models; multispecies system; serial transfer; theory.*

INTRODUCTION

Most of what is known of the dynamics of competitive interactions among species has been derived from laboratory studies. Most of these studies deal with two-species systems although Ayala (1972) found stable coexistence of three competing species of *Drosophila*. The analysis of three-species systems in the laboratory is a logical extension of the analysis of competition and more closely approximates the natural competitive situation.

The outcomes of competition involving three or more species need not follow from considerations of the dynamics of pairwise systems since emergent phenomena involving multispecies interactions may occur. Theoretical investigations (Gilpin and Ayala 1973, Gilpin 1974) have already suggested that a knowledge of the outcomes of competition between three, two-species pairs does not necessarily allow the prediction of the outcome of competition in the three-species system. In purely competitive systems, such emergent phenomena could take the form of coalitions in which two otherwise subordinate species would interact to suppress a third dominant species (Hairston et al. 1968). Gilpin (*unpubl. data*) has suggested that a mechanism involving population oscillations would lead to a stable multispecies system. If species A is dominant over B and B over C, but C is dominant over A, then stable limit cycles may

exist between the three competitors. The existence of immigration and/or refugia makes it impossible for one species to exclude the other completely. The three-species system will assume a stable cyclic pattern with species A driving B to low density, then C driving A to low density, and then B driving C to low density and so forth.

Another situation that would permit stability in three-species systems when not all the two-species systems were stable has been established by Gilpin and Ayala (1973). Ayala et al. (1973) and Gilpin and Ayala (1973) showed that the Lotka (1925) and Volterra (1926) model of interspecific competition failed to account for empirically demonstrated equilibria in several instances of competition between *Drosophila* species. Gilpin and Ayala (1973) suggested a modification of the classical model which incorporates a nonlinear self-interaction term. Their model is

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

where r_i is the intrinsic rate of increase of species i, N_i is the number of individuals of species i, K_i is the carrying capacity for species i, α_{ij} is the competition coefficient measuring the effect of an individual of species j on the rate of growth per individual of species i, and θ_i is a measure of the nonlinearity of intraspecific growth regulation.

The zero isosurfaces (loci of zero growth rate) for population densities following Eq. (1) are curved rather than straight as in the classical model. For
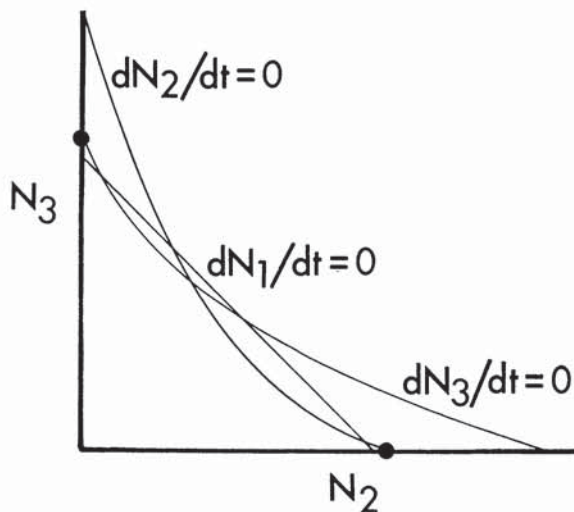
Fig. 1. Hypothetical model of three-species competition allowing for stable coexistence. Axes represent a phase plane whose coordinates are the numbers of individuals of each of two species. Zero isoclines for the three species are drawn on the phase plane. Solid circles show carrying capacities of species 2 and 3.

values of $\theta < 1$, the zero isosurfaces are concave upwards (Fig. 1). This permits two-species equilibria at points below a straight line connecting the carrying capacities of the two species. This is not possible under the conditions of the classical model (Ayala et al. 1973).

Concave upward zero isosurfaces permit stable

three-species systems to exist when not all the component two-species systems are stable. An example of this is shown in Fig. 1. Only the plane defined by the numbers of individuals of species 2 and 3 is shown. Since the zero isosurface of species 1 is below the carrying capacities for species 2 and 3, species 1 will not be able to coexist in a two-species system with either species 2 or 3. However, in the three-species system the zero isosurface of species 1 is above the point of stable coexistence between species 2 and 3 (i.e., the point of intersection between the isosurfaces). Thus, species 1 can invade this system and the three species may coexist stably even though the two-species interactions involving species 1 would not permit coexistence.

We have explored some of these possibilities by examining the behavior of a series of laboratory populations of three species of *Drosophila*. We report here an analysis of the data from this study and a discussion of their implications for the analyses of competition.

Materials and Methods

The species used in these experiments were *Drosophila willistoni* strain M11 (Mouráo and Ayala 1971), *Drosophila pseudoobscura* strain 211 (Ayala 1967), and a strain of *Drosophila nebulosa* collected in Belem, Brazil, around 1950 and consisting of the progeny of several wild collected females. Twenty-four populations consisting of all possible one-, two- and three-way combinations of these species were

TABLE 1. Experimental design, age of populations when terminated, and initial conditions for one-, two- and three-species populations. N = *D. nebulosa*, W = *D. willistoni*, P = *D. pseudoobscura*

Population no.	Temperature (°C)	Age (days)	No. flies used to start population		
			D. nebulosa	*D. willistoni*	*D. pseudoobscura*
N 10	22	184	600		
N 11	19	357	600		
W 10	22	350		600	
W 11	19	170		600	
P 10	22	350			600
P 11	19	197			600
NW 11	22	192	800	200	
NW 12	22	192	200	800	
NW 21	19	177	800	200	
NW 22	19	176	200	800	
PN 11	22	191	200		800
PN 12	22	191	800		200
PN 21	19	133	200		800
PN 22	19	133	800		200
PW 11	22	280		200	800
PW 12	22	280		800	200
PW 21	19	153		200	800
PW 22	19	203		800	200
PNW 11	22	191	150	150	300
PNW 12	22	192	300	150	150
PNW 13	22	192	150	300	150
PNW 21	19	133	150	150	300
PNW 22	19	126	300	150	150
PNW 23	19	126	150	300	150

TABLE 2. Mean numbers of flies and SE in single-species populations. All populations were begun with 600 flies

Species	Temp	N^a	Survivorship[b]	Recruitment[c]	Population size
D. willistoni	19	5	342 ± 39	135 ± 109	585 ± 39
	22	36	650 ± 31	459 ± 21	1108 ± 43
D. nebulosa	19	32	938 ± 27	477 ± 30	1415 ± 39
	22	15	489 ± 48	405 ± 58	874 ± 91
D. pseudoobscura	19	9	769 ± 19	230 ± 37	999 ± 31
	22	9	429 ± 26	182 ± 26	611 ± 41

[a] Number of weekly samples used to calculate means after equilibrium was obtained.
[b] Mean number of adult flies surviving in the population bottle after 1 wk.
[c] Mean number of newly-emerged adults added to the population bottle each week.

established at 19° and 22°C and maintained by serial transfer (Ayala 1965). The serial transfer technique provides for weekly estimates of survivorship, recruitment, and total population size. A population is begun by introducing adult flies into a 0.24-liter culture bottle containing 30 cm³ of Spassky's (1943) medium, and egg laying is allowed for 1 wk. The surviving adults are then counted under anesthesia and transferred to a fresh culture bottle. This process is repeated weekly. Adults that emerge in bottles where eggs were laid are collected and counted and added to the bottle containing the adult population on the same day that the adult survivors are censused and transferred. Bottles are discarded 5 wk after the first adults are introduced. A population consists of five bottles: one contains ovipositing flies, and four contain individuals in all stages of development.

Table 1 shows the experimental design and the number of individuals of each species used to initiate each population. Two different initial conditions were used for each two-species population and three for each of the three-species populations. Populations were maintained until either an equilibrium was obtained or one or two species were excluded.

RESULTS

The equilibrium numbers of flies in the single-species populations are given in Table 2. The determination of the point at which a population reaches equilibrium is somewhat arbitrary, but in most cases an examination of the curve of population numbers vs. time reveals a section where approximate equilibrium is reached (Ayala 1970). Initially, population size increases rapidly and expands beyond the equilibrium level. A rapid decrease in population size follows, after which nonrandom fluctuations in population number occur. In all cases we have used data from census periods following the initial "boom and crash" to calculate equilibrium values for survivorship, recruitment, and population size.

The general outcome of competition in all the populations containing two or three species is given

in Table 3. With the exception of population NW11, *D. nebulosa* and *D. willistoni* are capable of coexisting at both 19° and 22°C. Despite the fact that populations NW21 and NW22 were begun with quite different frequencies of the two species (Table 1), both populations have reached similar equilibrium sizes (Table 4). This indicates that the equilibrium is stable, as is the case for other species pairs previously examined (Ayala et al. 1973).

Those populations involving competition between *D. pseudoobscura* and *D. nebulosa* (PN11, 12, 21, 22) did not result in an instance of stable coexistence. In PN11, *D. nebulosa* was effectively eliminated (5

TABLE 3. General outcome of competition in populations begun with two and three species

| Population no.	Days before termination	Result
NW 11	192	*D. nebulosa* eliminated
NW 12	192	Equilibrium
NW 21	177	Equilibrium
NW 22	176	Equilibrium
PN 11	191	*D. nebulosa* eliminated
PN 12	191	Both species present, wide population fluctuations
PN 21	133	*D. nebulosa* eliminated
PN 22	133	*D. nebulosa* eliminated
PW 11	280	Equilibrium
PW 12	280	Equilibrium
PW 21	153	*D. willistoni* eliminated
PW 22	203	Equilibrium
PNW 11	191	*D. nebulosa* eliminated, (*D. pseudoobscura*, *D. willistoni* present at termination)
PNW 12	192	*D. nebulosa* eliminated, (*D. pseudoobscura*, *D. willistoni* present at termination)
PNW 13	192	*D. nebulosa* eliminated, (*D. pseudoobscura*, *D. willistoni* present at termination)
PNW 21	133	*D. nebulosa*, *D. willistoni* eliminated
PNW 22	126	*D. nebulosa*, *D. willistoni* eliminated
PNW 23	126	*D. nebulosa*, *D. willistoni* eliminated
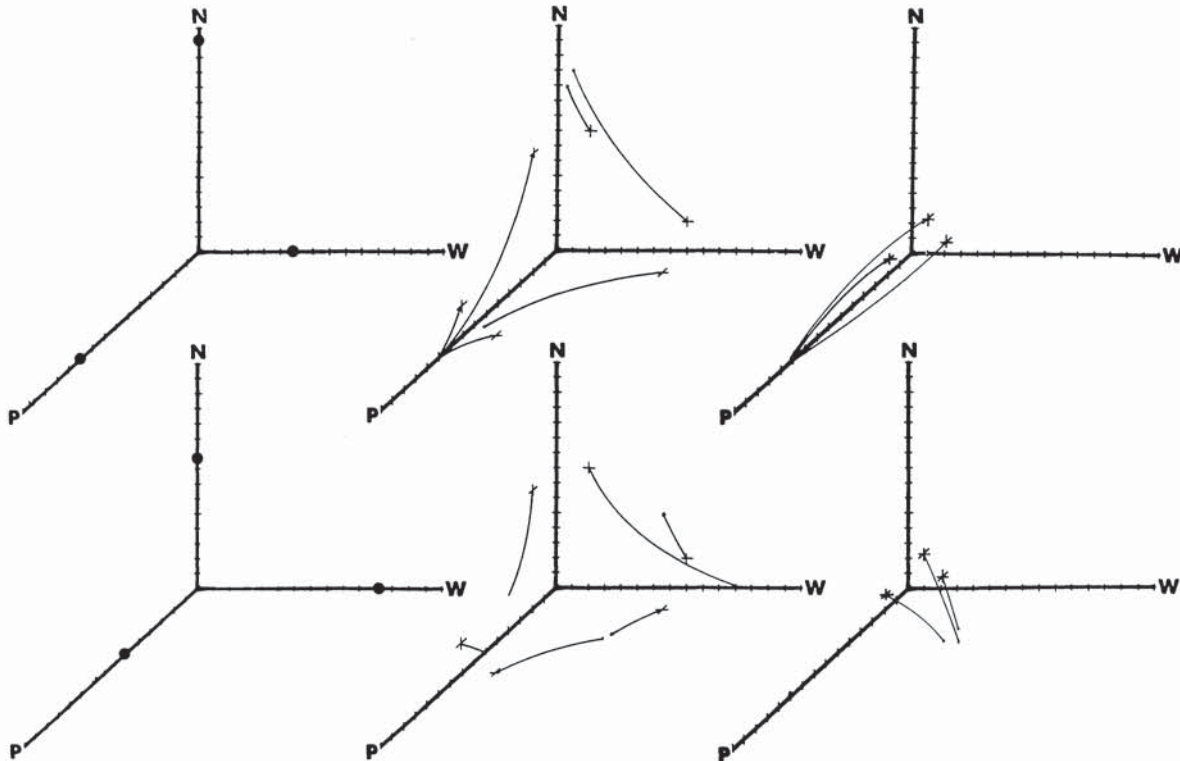
Fig. 2. Schematic summary of experiments. First row gives results of experiments at 19°C, while the second row gives the 22°C series. Left-hand column gives results of single-species experiments. Solid circles indicate carrying capacities of the three species. Middle column gives the results of the two-species experiments; crosses indicate initial numbers of individuals, and the curved lines show subsequent trajectory of the system. Right-hand column gives results of the three-species experiments; stars indicate initial conditions, and the curved lines show subsequent trajectory of the system. Actual trajectories in the two- and three-species systems were somewhat irregular.

individuals in 850) after 155 days of competition. *Drosophila nebulosa* was absent from populations PN21 and PN22 after 119 days. In PN12, both species maintained substantial population numbers, but no equilibrium level was reached, primarily because of wide fluctuations in the numbers of *D.*

pseudoobscura. It is likely that a temperature higher than 22°C would result in coexistence between *D. nebulosa* and *D. pseudoobscura* since *D. nebulosa* is a neotropical species whereas *D. pseudoobscura* distribution is restricted primarily to North America.

Three of the four populations begun with *D.*

TABLE 4. Mean numbers of flies and SE in two-species competition populations reaching equilibrium

Population no. and temp (°C)	Species	N^a	Survivorship	Recruitment	Population size
NW 12 22°	D. nebulosa D. willistoni	13	199 ± 23 330 ± 32	190 ± 22 293 ± 32	389 ± 38 623 ± 50
NW 21 19°	D. nebulosa D. willistoni	14	724 ± 76 46 ± 7	397 ± 33 22 ± 2	1121 ± 94 68 ± 8
NW 22 19°	D. nebulosa D. willistoni	13	805 ± 38 82 ± 21	433 ± 48 40 ± 10	1238 ± 54 122 ± 29
PW 11 22°	D. pseudoobscura D. willistoni	30	225 ± 14 375 ± 20	107 ± 13 309 ± 19	332 ± 15 684 ± 34
PW 12 22°	D. pseudoobscura D. willistoni	30	248 ± 45 347 ± 5	121 ± 15 262 ± 18	369 ± 22 609 ± 41
PW 22 19°	D. pseudoobscura D. willistoni	15	545 ± 30 27 ± 4	152 ± 20 22 ± 4	706 ± 30 49 ± 5

[a] Number of weekly samples used to calculate means after equilibrium was obtained.

willistoni and *D. pseudoobscura* came to an equilibrium with both species present. This result confirms the findings of Ayala (1972) and Ayala et al. (1973). Ayala et al. (1973: Table 1) gave equilibrium population sizes for these two species at 21.5°C which are remarkably similar to those obtained by us at 22°C (PW11 and PW12, Table 4). These two sets of data are essentially replicates since the same strains of each species were used in both cases. The similarity of results obtained in these and earlier experiments suggests that the system is highly deterministic.

In all populations involving three species, *D. nebulosa* was eliminated (Table 3). In addition, *D. willistoni* was eliminated from the three-species populations kept at 19°C, which resulted in single-species equilibria. At 22°C *D. willistoni* and *D. pseudoobscura* were present when the three populations were discarded. All three populations showed wide fluctuations in the numbers of these two species after the elimination of *D. nebulosa*. Presumably two-species equilibria would have been reached in these populations had they been maintained for a longer time.

Figure 2 graphically summarizes the results of these experiments. The axes of the coordinate systems represent the numbers of each species. These plots giving the results of two- and three-species experiments (columns 2 and 3) show the smoothed trajectories the populations followed in coming to an equilibrium point.

DISCUSSION

None of the six populations begun with three species reached an equilibrium at which all three species were present. The results of the two-species experiments were adequate predictors of the three-species experiments. At 19°C *D. pseudoobscura* eliminated *D. nebulosa* from two-species populations and came to equilibrium with *D. willistoni* in one of two populations. *Drosophila nebulosa* and *D. willistoni* coexisted stably at 19°C. In three-species populations, *D. pseudoobscura* eliminated both *D. nebulosa* and *D. willistoni*. A stable three-species population might have resulted if *D. nebulosa* and *D. willistoni* had been able to act synergistically against the dominant *D. pseudoobscura*. In the 22°C series of populations, *D. pseudoobscura* eliminated *D. nebulosa* from two-species populations and came to equilibrium with *D. willistoni*. *Drosophila willistoni* eliminated *D. nebulosa* from one population and came to an equilibrium in the second population. Under three-species conditions, *D. nebulosa* was eliminated from the populations while both *D. pseudoobscura* and *D. willistoni* were present at the termination of the experiment. Again the results of

the two-species experiments were adequate predictors for the three-species experiment.

Results qualitatively similar to these were found by Vandermeer (1969) in his analysis of competition among four species of ciliate protozoans. Vandermeer could find no evidence for higher order interactions involving more than two species and was able to use competition coefficients in two-species systems to predict the outcome of four-species competition. Hairston et al. (1968) did find evidence for interaction effects among three species of *Paramecia* in an experimental community comprised of species of bacteria and protozoa. Wilbur (1972) studied the competitive relationships among three species of salamanders (*Ambystoma*). He found evidence that competition among salamander larvae involves higher order interactions among species and their proportions and densities. Neill (1974) presented evidence that competition coefficients change as a function of the species composition in aquatic microcrustacean communities.

Under the experimental conditions used in the present study, we have found no evidence of species interactions involving either limit cycle models or models postulating interference between species. Similarly the conditions necessary for three-species coexistence under the Ayala–Gilpin (1973) model are not met in these experiments. Our results do, however, suggest that competition in multispecies systems may often result from a linear superposition of pairwise interactions. A knowledge of the two-species interactions among competitors may give a rather complete description of a multispecies system.

The data provided in Tables 2 and 4 may be used to calculate competition coefficients on the assumption that the systems follow the Lotka-Volterra formulations. Under this model a necessary condition for a stable equilibrium is that the product of competition coefficients, $\alpha_{12} \cdot \alpha_{21}$, is less than 1.0. This product exceeds 1.0 (1.98 and 4.52) in two of the six cases given in Table 4. Ayala et al. (1973: Table 1) gave competition coefficients for eight, two-species systems that were stable. In only one of these cases would the Lotka-Volterra model have predicted a stable equilibrium. Thus, of a total of 14 stable two-species systems, five are consistent with the Lotka-Volterra model. Our data, therefore, support the contention of Ayala et al. (1973) that the Lotka-Volterra model may often be insufficient to explain the dynamics of two-species competition.

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