chapter 2

The Assembly of a Laboratory Community: Multispecies Competition in *Drosophila*

Michael E. Gilpin, M. Patricia Carpenter, and Mark J. Pomerantz

LABORATORY RECONSTITUTION OF COMMUNITIES

For the last eight years we have been studying laboratory systems assembled from about 30 species of *Drosophila* flies. Our motivation for this effort has been as follows. While the ultimate goal of community ecology is to understand actual communities, the direct study of these communities outdoors labors under crippling disadvantages. In the field, environmental parameters vary uncontrollably in time and in space, inordinate numbers of plant and animal species are present, the individual life histories of most of these species and their interactions in pairs or in larger sets are poorly known, and experimental manipulations may be infeasible or doomed to yield ambiguous results (Bender et al. 1984). In the laboratory, one can specify and hold constant the values of environmental parameters, limit the number and identities of species present, and carry out experimental manipulations with few constraints. These facts make it self-evident that it will be difficult or impossible to understand field communities until one has mastered the easier task of understanding laboratory communities.

Unfortunately, much of the previous work on laboratory communities has used systems too grossly simplified to have relevance to the real world. There have been too few species with too little interesting behavior (typically two species, often microorganisms), and too few attempts to mimic environmental variation. The purpose of this chapter is to illustrate how realistically complex communities can be synthesized in the laboratory and how they can be used to address one set of issues currently facing field ecologists: the questions posed by multispecies competition.

Our approach is community reconstitution, the construction of communities from individual parts. We believe that the acid test of one's understanding of any complex system—whether it be a clock, a virus, or an ecological community—comes in trying to reassemble the system out of its pieces. Reconstruction is *the* procedure that accounts for many of molecular biology's successes, for instance, reaching an understanding of mitochondrial function by isolating individual enzymes and soluble factors and by recombining

them until the electron transfer ability of the whole mitochondrion has been recreated. Besides offering in our view an essential route to understanding ecosystems, reconstitution is also of growing practical importance to field ecologists faced with the task of restoring damaged ecosystems (Gilpin 1983).

QUESTIONS OF STRUCTURE IN MULTISPECIES COMPETITION

In this chapter we address five problems concerning multispecies competition.

1. Transitivity of interspecies competition Recently there has been extended discussion of pairwise competitive relationships in field systems. Most investigators have found so-called transitive dominance relationships in various phyla, i.e., species A beats species B, B beats C, *and* A beats C (Kato et al. 1963, Hairston et al. 1968, Vandermeer 1969, Lang 1973, Connell 1978, Luckinbill 1979, Goodman 1979). Undisturbed intertidal communities (Connell 1961a, Dayton 1971, Paine 1974) along with many plant successions (Horn 1981, Connell 1978) have a single dominant competitor, which also implies transitivity. Nonetheless, there are theoretical reasons, based on interference competition relationships (Gilpin 1975), to expect competitive intransitivities such that A beats B, B beats C, *but* C beats A. Indeed, Buss (Chapter 31; see also Jackson and Buss 1975, Buss and Jackson 1979) has found intransitive relationships in subtidal communities. How can one rationalize these varying outcomes?

2. Mechanisms of competition Ecologists have often categorized competition as being of two types: the dichotomy of "r" and "K" competition (MacArthur and Wilson 1967) or the related dichotomy of "scramble" and "contest" competition. Both of these dichotomies correspond roughly to Miller's (1967) distinction between the rapid exploitation of resources in a competitively unsaturated environment and the efficient utilization of or control over resources in a saturated environment. We prefer to discuss the somewhat related dichotomy of "exploitation" and "interference" competition (Case and Gilpin 1974). The former term involves the flow of resources from a lower trophic level. The latter term involves direct behavioral interference (by aggression, allelochemicals, or usurping space) against an exploitation competitor, thereby increasing the flow of resources to the species that successfully interferes.

In a multispecies system of competitors, a further dichotomy regarding interference competition must be considered (Case et al. 1979): "generalized" and "specific" interference. We define generalized interference as an action that affects all (or all other) species in a relatively uniform manner, such as habitat destruction or release of a nonspecific poison. Generalized interference may be mathematically represented as the introduction of a negative resource: the more of it exists, the worse all other species do. A general lowering of equilibrium densities of all other species following introduction of a new species would suggest operation of generalized interference. Specific interference, on the other hand, is a negative interaction that affects only one or a subset of the competing species, such as a specific poison, aggression, predation on juveniles, or rape directed at a particular species.

The presence or absence of interference competition of either form affects many of the other questions that we are asking. For instance, specific interference favors the creation of intransitive competition relationships (see discussion below); this makes the reconstitution approach difficult, since each instance of specific interference has to be treated on an ad hoc basis.

3. Niche dimensionality The idea of niche dimensionality is an old one that has at least three different meanings in ecology. One use, which we shall not employ in this chapter, is that of Cohen (1978), who applied the term "dimensionality" to certain properties of food webs. A second, older use is the dimensionality of the fundamental niche, which involves the number of factors limiting the growth of the species population and which has been linked to questions of coexistence among species (Hutchinson 1978). Finally, we shall use the word dimensionality to refer to the number of independent measures of

single-species population growth needed to assess interspecific competitive ability.

4. Assembly rules and alternative domains of attraction From empirical patterns of bird species co-occurrences on Southwest Pacific islands, Diamond (1975) induced a set of so-called assembly rules that specified which species combinations were forbidden and which were permitted to occur in nature. These empirical patterns imply that alternative stable communities can be assembled from a certain species pool under a given set of environmental conditions. Gilpin and Case (1976), working with an algorithmic model of interspecies competition, explored theoretically how the expected occurrence of such alternative stable communities should depend on total pool size and on the mean strength of the competition coefficient (alpha). Those theoretical results are consistent with Diamond's empirical observations and suggest interspecies competition as a possible mechanism, although Diamond discussed other contributing factors as well. The theoretical literature refers to such alternative stable communities as "multiple stable points" or "multiple domains of attraction."

The existence and interpretation of assembly rules have been debated on two grounds. First, Connor and Simberloff (1979) questioned Diamond's empirical conclusions for statistical reasons. However, Diamond and Gilpin (1982; Gilpin and Diamond 1984) showed that these statistical objections were invalid and that a proper statistical analysis confirmed the reality of permitted and forbidden combinations. Second, Connell and Sousa (1983) dismissed evidence for alternative community structure derived from observation of natural communities. They called instead for evidence from experimental perturbation studies. For instance, one could defaunate replicated habitat patches and observe whether alternative communities developed. Our laboratory *Drosophila* system permits us to carry out such an experimental test for alternative communities, but with a decisive advantage over field tests. If alternative communities did develop in the field, this might merely reflect undocumented differences in the identities of the colonizing species arriving at different experimental plots. In the laboratory we have complete control over the "colonizing" species, permitting us to separate the contributions of colonization and post-colonization events to the creation of alternative communities.

5. Prediction Predicting the structure of an ecological community obviously involves more complications than do predictions in some other areas of science, such as predicting the next return date of Halley's comet. We believe that two related issues are involved.

First, there is a quantitative issue. Physicists pretend that the only real prediction is a quantitative one, although in reality they expect much higher precision for predicting the absorption spectrum of a hydrogen atom than the location, date, and Richter scale value of future earthquakes in California. Paine (1980), implicitly using the standard of hydrogen atoms rather than earthquakes, concluded that long-term predictions of population sizes are almost certain to be impossible for ecologists. In our view, ecological predictions suffer under a curious but understandable schizophrenia caused by differences between theories and field observations, and ecologists should learn from what physicists do rather than from what they pretend to do. Theoretical models of populations are almost always cast in terms of absolute population densities, while field observations are normally in far more relative terms such as presence absence or rank order of abundance. The precision of quantitative prediction possible for our laboratory system will suggest limits to realistic expectations for field systems.

Second, and more interesting to us, are questions about whether knowledge of the parts predicts properties of the whole. For instance, can one predict community structure from studies of pairwise interactions? Can one predict the outcome of pairwise interactions from studies of separate species? If the answer is yes in either case, how many parameters are needed? Theory and some laboratory studies suggest that measures of fundamental niche properties (i.e., of the niches of species studied in isolation) *might* yield predictions of the realized niche attained in the presence of competing species. For instance, the

theoretician may assume a one-dimensional resource space and draw single-species utilization curves whence derive all predictions of community structure: e.g., species packing depends on the width of the resource utilization niche (see examples in Roughgarden 1979). Lending support to this hope, laboratory studies of microorganisms limited by a single nutrient have shown that a species' half-saturation concentration for nutrient utilization suffices to predict that species' position in the competitive hierarchy (Hsu et al. 1978). These considerations suggest that there might be a single key to predicting community structure. On the other hand, interference competition permits an infinite variety of special cases and intransitivities, while even exploitation competition is unlikely to reveal a single limiting factor over which species assort.

Thus, only empirical studies, beginning with laboratory studies, can reveal the quality and precision of predictions attainable in ecology.

THE *DROSOPHILA* MODEL

The Species Table 2.1 gives the taxonomic names, abbreviations, geographical distribution, and climate preference of the 28 species that we studied.

Since our laboratory *Drosophila* community is to be used as a model for field communities, we

Table 2.1 THE 28 SPECIES USED IN THIS STUDY

Genus and subgenus	Group	Subgroup	Species	Abbreviation	Distribution
Drosophila					
Drosophila	Annulimana		*gibberosa*	Gib	NW TR
	Funebris		*funebris*	Fun	C TE
	Immigrans		*immigrans*	Imm	C TE
			quadrilinecta	Quad	WPI TE
	Mesophragmatica		*gaucha*	Gau	SAM TE
	Pallidipennis		*pallidipennis*	Pallid	NW TR
	Repleta	Hydei	*hydei*	Hyd	C TE
		Mercatorum	*mercatorum*	Merc	NW TE
	Robusta		*robusta*	Rob	NW TE
	Virilis		*virilis*	Vir	OW TE
Sophophora	Melanogaster	Ananassae	*ananassae*	AnB	C TR
		Eugracilis	*eugracilis*	Eug	SEA TR
		Melanogaster	*melanogaster*	MelS	C TT
			simulans	SimA	C TT
		Montium	*birchii*	Bir	ANG TR
			serrata	Ser	ANG TT
	Obscura		*persimilis*	PerO	NAM TE
			pseudoobscura	Psd	NAM TE
	Saltans		*prosaltans*	Pro	NW TR
			sturtevanti	Stv	NW TR
	Willistoni		*equinoxialis*	Eqx	NW TR
			insularis	Inw	NW TR
			paulistorum	Paul	NW TR
			tropicalis	Trop	NW TR
			willistoni	W(+)	NW TR
			willistoni	WW	NW TR
			nebulosa	Neb	NW TR
Zaprionus			*vittiger*	Zap	WAF TR

Genus (italicized) and subgenus (not italicized) names are given in column 1, group and subgroup names in columns 2 and 3, species names (italicized) in column 4, abbreviated names used in this chapter in column 5. WW and W(+) are the same species, but WW is the white-eye mutant.

The first characters in the distributional code give location: ANG = Australia and New Guinea; C = cosmopolitan; NAM = North America; NW = New World; OW = Old World; SAM = South America; SEA = South East Asia; WAF = West Africa; and WPI = West Pacific Islands. The second part of the code gives the climate preference of the species: TR = tropical; TE = temperate; and TT = tropical and temperate.

must initially consider what mappings are possible from bottle to field. Clearly, this depends on the range of behaviors of our *Drosophila* system. *Drosophila* do compete under both r and K conditions. They exhibit mechanisms of exploitation competition, generalized interference, and specific interference. Among these mechanisms are adult food preferences (Sang 1949; Merrell 1951; Buzzati-Traverso 1949; da Cunha et al. 1951, 1957; Cooper 1960), oviposition site preferences (Moore 1952, Del Solar and Palomino 1966, Del Solar 1968, Barker 1971), pupation site preferences (Barker 1971, de Sousa et al. 1968, Sameoto and Miller 1968), interspecific "rape" leading to sterile eggs (Narise 1965), poisonous larval metabolites (Weisbrot 1966, Dawood and Strickberger 1969, Budnik and Brncic 1976), larval alterations of mechanical properties of the medium that affect survivorship, and differences in larval food preferences and feeding rates (Lindsay 1958, Cooper 1960, Bakker 1961, Gilpin 1974). All these mechanisms permit both high niche dimensionality and competitive intransitivities. Nothing about *Drosophila* excludes assembly rules and multiple domains of attraction. Very little is either ruled out or necessarily ruled in. Thus, a finding, say, that increased resource heterogeneity permits greater coexistence is unlikely to be based in a simple laboratory artifact. In short, we know of no other laboratory system that realistically addresses so many ecological problems for so little time, energy, and expense.

The Environment The bottles that delimited the laboratory environment of the flies were ¼-pint cream bottles. Most often, the food was a 40-ml plug (about 1 cm deep) of the standard mixture of cornstarch and molasses, laced with proprionic acid and tegosept for mold and bacteria control. We term this system "thick food." However, in some of the work reported here we used different food structures and amendments. A second system, which we dubbed "thin food," consisted of only 3 ml of standard medium atop a 10-ml plug of agar. This food layer was only about 1 mm deep, less than the length of a third instar larva and was, in most cases, totally consumed prior to the onset of pupation. Generation times were thus shorter and these systems were more sensitive to the slight temporal variability in bottle humidity, microflora, etc. In thick-food systems the actual limitation on population sizes could not be the energy in the food, as most of this was still remaining after fly production ceased (Gilpin 1974); hence competition for space, interference competition, or availability of protein may instead be limiting. In thin-food systems the food itself is definitely limiting; whether it is the sole limiting factor is uncertain.

These thick-food and thin-food systems were each run at both 25°C (tropical) and 19°C (temperate) temperatures. These temperatures represent physiological limits for some of the fly species, as mating behavior and egg laying are both quite temperature-sensitive in *Drosophila*. For instance, species Psd (*D. pseudoobscura*) is torpid at 25°C but is fourth in the dominance hierarchy in the thick-food system at 19°C.

A somewhat different system, which we dubbed the "augmented system," had two tablespoons of puffed millet upon which was poured 30 ml of the standard medium. These millet balls perhaps supplied a different nutrient. More importantly, however, they altered the medium's surface texture and its "soupiness" under larval activity, thereby possibly influencing the interference interaction of larval drowning.

By virtue of more experimental effort and replications, the 25°C thick-food system can be considered the baseline, with the other experimental treatments seen as perturbations (sensitivity studies) away from it.

Types of Experiments In all experiments adult flies were anesthetized, sexed, and counted into culture bottles. The adults were always removed from the bottle before any progeny (also called recruits or F1s) from the next generation started to emerge (eclose) from their pupal casings. Normally, this removal was done at the seventh day following the introduction. Recruits were then removed at later days or, more typically, weeks. Bottles normally produce recruits for five weeks, during which time the food hardens and excrement accumulates on the inside of the glass bottle. Thus, each bottle "ages" over the course of an experiment.

The experiments reported below were of two general types: short-term and long-term. Short-

term experiments lasted less than a single generation. Adults were added to a bottle, and all surviving adults and recruits in that bottle were sacrificed and counted at later times. (Ayala et al. [1973] refer to these as input-output or type II experiments.) The three experiments described below to measure single-species parameters (larval production, life history parameters, and population dynamics) used this technique and were carried out solely with thick-food systems.

Long-term experiments involved multiple generations and were carried out with the serial transfer technique (Ayala 1967). A system begins with a single bottle to which adults are added. After one week, a new bottle is added and the surviving adults are transferred to it, usually without anesthetization or counting. After the second week, a third bottle is added to the system, and the surviving adults in the one-week-old bottle (the second bottle) and the recruits in the two-week-old bottle (the first bottle) are transferred to it. Similarly, after the third or fourth week a new fourth or fifth bottle is added, and all adults or recruits in the system are transferred to it. Since bottles cease to produce new recruits after the fifth week, a steady state is reached then: a new bottle is added, but the first bottle can be discarded. Thus, from the end of the fifth week onward the system consists of five bottles of different ages, ranging from one to five weeks. (Ayala et al. [1973] refer to these as type I experiments.) These long-term experiments usually ran for 19 or 24 weeks or, in some cases, until the conclusion was obvious. This technique was used for the two experiments on pairwise competition and on multiple domains of attraction.

We now describe each of these individual experiments.

SHORT-TERM EXPERIMENTS

Larval Production Rate In these experiments we started 25 replicate bottles of thick food, each with 100 adults of a single species. At day 6 we removed the adults, liquified the media by boiling the bottles in a microwave oven, and separated the larvae in a 10% sucrose solution. We then dried this larval population in a vacuum oven and obtained its total dried weight, which we took as a measure of larval production. It represents an integration of the egg laying rate times the growth rate of an individual larva and was determined for each of the 28 species at 25°C and at 19°C. We refer to this measure as the variable LARVPROD.

Life History Parameters Twenty-five replicate adult populations of 13 pairs of a single species were placed in glass shell vials 25 mm in diameter at 25°C. They were given four days to oviposit, after which the adults were removed and the vials monitored on a twice-daily basis for appearance of first, second, and third instar larvae and for pupae. At each monitoring the newly emerged adults were removed and counted, to preclude a second generation. The monitorings and removals continued until after all larval activity ceased (about 6 weeks). Fig. 2.1 illustrates the results of these experiments for the species Psd and Zap. From the emergence curve, which is the average number of newly emergent adults per day, five variables describing life history can be read off: REPLLH, a measure of the replacement (the area under the emergence curve divided by the number of starting adults); RLH, a measure of the exponential rate of increase based on the replacement and the generation time; FSTEMGLH, the day of first emergence; PKEMGLH, the day of peak emergence; and MAXEMGLH, the maximum daily rate of emergence.

Estimates of Growth Parameters Replicate bottles of thick food were initialized with adults of one species over a span of densities designed to run from roughly 10% to 150% of the estimated carrying capacity. This starting population size is denoted N_t. At the end of one week the surviving adults were counted, while the recruited F1s were removed and counted at the end of the second, third, fourth, and fifth weeks by the techniques described by Ayala et al. (1973). The sum of the surviving adults at week 1 and the recruits at weeks 2 to 5 gives an estimate of the total population size after one generation, denoted N_{t+1}. This experiment was carried out for each of the 28 species at 19°C and at 25°C.

The parameters of discrete growth equations

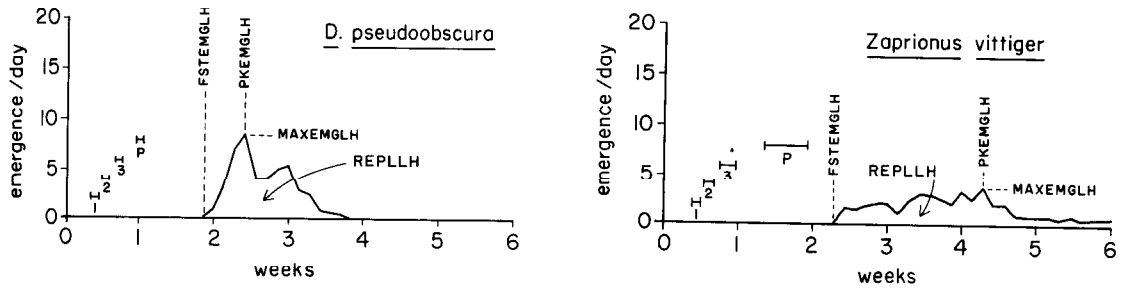

Fig. 2.1 Sample of results from short-term life history experiments. Thirteen pairs of adults of each species were placed in a vial and were removed after laying eggs for four days. Vials were examined twice daily for the presence of first (1), second (2), and third (3) instar larvae and for pupae (P); the horizontal bars in the lower left corner of each graph give the 65% confidence intervals for the presence of these four life stages. Newly emerged adults were removed each day for the first 42 days, and the average emergence of new adults per day is plotted on the ordinate. From these emergence curves one can read off the day of the first emergence (FSTEMGLH), the day of peak emergence (PKEMGLH), the maximum daily rate of emergence (MAXEMGLH), and the replacement (REPLLH: area under curve ÷ number of initial adults). The emergence curve for *D. pseudoobscura* at 19°C is "peaked," while that for *Z. vittiger* at 19°C has a "plateau" shape.

can be extracted by fitting these values of N_t and N_{t+1} to the equation

$$N_{t+1} = N_t + rN_t[1 - (N_t/K)^\theta] \qquad (2.1)$$

where K is the single-species equilibrium density or the carrying capacity of the environment, r is the rate of growth at low density, and θ is a measure of the asymmetry of the growth curve (Pomerantz et al. 1980, Thomas et al. 1980). There is a possible degeneracy in the simultaneous estimation of r and θ, but their product $r\theta$, which is the stability parameter for this system (see appendix C in Pomerantz et al. 1980), is free of this regression pathology. In the analysis and tables below we use KFIT, RFIT, and RTFIT to stand, respectively, for these extracted values of K, r, and $r\theta$.

There were two additional measurements that we made on each species. First, in order to be able to correct for size differences among species, we reared flies under moderate crowding and obtained the average dry weight of one individual (the variable DRYWT). Second, in long-term experiments we counted the number of individuals of a victorious species at the end of a pairwise competition trial (after at least 15 weeks; see below for a more detailed explanation) to obtain an alternative measure of carrying capacity for that species. For species that were usually eliminated in pairwise competition, we obtained this alternative measure (termed K-15) from serial transfer systems that we ran for 15 weeks before counting the number of flies.

LONG-TERM EXPERIMENTS

In the long-term experiments for both single- and multispecies systems, surviving adults and recruits from older bottles were transferred without counting to a fresh bottle of medium. Experiments were generally run for 19 weeks at 25°C and 24 weeks at 19°C. These times amount to roughly 10 generations and were selected because exclusions usually occurred in considerably shorter times and coexistences were maintained for considerably longer times.

Pairwise Competition Serial transfer systems were started with 13 male-female pairs of each of two species. This was done for all possible pairings of all 28 species ($28 \times 27/2 = 378$ pairings) at 19 and 25°C for the thick-food system; for all pairings of 20 species ($20 \times 19/2 = 190$ pairings) at 19 and 25°C for the thin-food system; and for all pairings of 10 species ($10 \times 9/2 = 45$ pairings) at 25°C for the augmented system. Each pairing was replicated two or three times. The flies were not counted at the weekly transfers. Because the different species could be distinguished visually, the possible absence of one of

the competitors was noted; after five weeks of such a species's absence the system was terminated and the adult flies counted.

Multiple Domains The remaining long-term experiment was done with 30 different serial transfer systems, using thick food at 25°C and initialized with varying densities of 10 different species: Merc, Ser, Zap, Paul, Neb, Psd, WW, Imm, Eug, and Gib. To increase the total size of the mixed species population, we used three bottles connected by plastic tubing in place of each single bottle normally used in the serial transfer experiments. That is, in the steady state after five weeks there were fifteen bottles in the system: three each of one-week-old, two-week old, three-week-old, four-week-old and five-week-old bottles. The starting population was mixed and divided into thirds to begin the experiment, and at each transfer the flies were again mixed and divided into thirds. The systems were run for 35 weeks. This experiment is analogous to the relaxation of a supersaturated fauna on a land-bridge island, in that the system is initially stocked with more species than can be retained, with the result that species go extinct.

The initial conditions for the 30 different systems were as follows. In 10 systems the starting numbers of the 10 species were 910, 10, 10, . . . , 10 individuals, with each of the 10 species started once at 910 individuals (91% frequency) in order to explore all "corners" of the system's state space. For the other 20 systems, the initial densities were chosen randomly according to the scheme used by Gilpin and Case (1976) in their computer work on multiple domains of attraction in competition communities. This scheme was in effect a broken stick model, with the line segment (0,1000) broken at nine randomly chosen points and the lengths of the 10 resulting segments taken as the starting densities. In no case were fewer than 5 females and 5 males of a species used in an initialization.

BEHAVIOR OF THE MODEL

Single-Species Studies

Studies at 25°C Table 2.2 summarizes the results of all of our single-species work at 25°C, the temperature selected for intensive study because of faster development times. Table 2.3 gives the correlations between these single-species parameters. (The last two columns of Tables 2.2 and 2.3 are derived from pairwise competition studies and are discussed in the next section.)

Five parameters measure adult production: MAXEMGLH, the maximum rate of emergence of F1s; the replacement REPLLH; the rate of increase RI.H; and K-15 and KFIT, the two alternative measures of carrying capacity. (The carrying capacities are heavily influenced by adult production because adult survival is less than 20% per week, so that a high production rate is needed to sustain a high carrying capacity.) There is close concordance among these five measures of adult production: the 10 pairwise correlation coefficients among them all fall between 0.49 and 0.88 and average 0.74 (Table 2.3). Not surprisingly, the correlation between the two measures of carrying capacity is especially high (0.87).

Larval production (LARVPROD) also correlates positively with these five measures of adult production, but more weakly: the five coefficients range from 0.23 to 0.38 and average 0.31. One reason why larval and adult production correlate only weakly is that larvae, though numerous, may not reach the critical weight threshold for pupation (cf. Gilpin's and McClelland's [1979] model for the pupation threshold of *Aedes aegypti*). A second reason is that high larval production may actually interfere with pupation: many larvae pupate on the surface of the medium and are drowned by subsequent larvae. Both reasons mean that larval production is not guaranteed to translate one-for-one into adult production.

The variables FSTEMGLH and MAXEMGLH both correlate negatively with all five measures of adult production as well as with larval production. Small values of these variables (day of first and peak emergence, respectively) mean early emergence. Thus, early emergence favors high larval and adult production.

Studies at 19°C Similar data were collected at 19°C for all species except W(+). Qualitatively, the 19°C data are similar to those at 25°C. Quantitatively, development (e.g., FSTEMGLH and PKEMGLH) was slower at 19°C for 25 of the 27

Table 2.2 SINGLE-SPECIES DATA AND COMPETITIVE RANKS FOR ALL 28 SPECIES ON THICK FOOD AT 25°C

Species	KFIT (flies)	RFIT (flies/wk)	RTFIT	RLH (flies/d)	REPLLH	FSTEMGLH (day)	PKEMGLH (day)	MAXEMGLH (flies/day)	LARVPROD (mg)	K-15 (flies)	DRYWT (0.1 mg)	COMP	RANK
AnB	556	4.5	1.22	.044	1.67	10	11	12	28.3	685	1.60	.497	15
Bir	422	7.9	.95	.025	1.52	12	14	5	12.6	411	1.7[illegible]	.160	24
Eqx	704	4.1	1.30	.051	1.92	11	13	14	19.7	560	1.20	.698	10
Eug	481	1.8	1.26	.016	1.21	9	11	4	35.4	472	1.75	.276	20
Fun	248	21.2	1.1	.030	1.79	14	15	5	6.0	325	5.29	.537	14
Gau	312	1.4	.92	.000	.98	16	19	7	1.7	312	4.89	.014	28
Gib	136	1.0	.77	.009	1.21	18	20	3	60.3	110	8.20	.275	21
Hyd	295	5.9	.89	.048	3.43	16	17	6	19.2	382	5.50	.964	2
Imm	191	829.7	.83	.017	1.39	13	14	4	5.9	216	5.59	.064	27
Ins	645	2.6	.98	.071	2.84	12	14	17.5	27.4	635	1.53	.713	8
MelS	737	6.7	1.34	.114	4.76	10	14	23	63.1	894	2.53	.997	1
Merc	441	840.9	.85	.028	1.79	13	15	6	26.8	399	4.06	.749	6
Neb	459	13.9	.97	.076	3.72	11	13	10	55.4	199	2.29	.526	12
Pallic	79	771.0	.77	.014	1.13	14	17	3	2.0	171	4.84	.137	25
Paul	485	26.5	1.06	.079	3.35	10	12	10	26.6	576	1.6[illegible]	.696	11
PerO	124	872.1	.87	.031	1.86	16	21	7.5	10.0	30	3.20	.065	26
Pro	273	2.0	.93	.041	2.54	14	22	7	13.4	248	2.10	.355	19
Psd	261	2.0	.89	.068	3.27	13	16	14	8.9	301	3.17	.484	16
Quad	320	3.3	.99	.000	.98	11	13	5	12.7	243	4.06	.232	22
Rob	238	1.1	1.26	.011	1.27	15	20	3	9.6	160	6.4[illegible]	.209	23
Ser	592	809.3	.81	.079	4.14	12	14	17	18.7	402	1.89	.421	17
SimA	593	6.6	1.13	.078	2.70	9	11	12	52.7	497	2.15	.898	3
Stv	233	1087.4	1.09	.038	2.98	18	25	5	58.7	285	2.49	.797	5
Trop	979	9.2	1.02	.080	3.12	10	13	18	38.8	607	2.09	.762	7
Vir	621	10.9	1.09	.088	6.63	13	16	15	15.8	645	4.68	.904	4
W(+)	576	7.5	1.13	.049	2.01	10	12	11	30.7	620	2.27	.759	9
WW	430	986.9	.99	.053	1.98	10	12	10	17.7	442	1.58	.419	18
Zap	264	6.0	.84	.017	1.45	12	14	2.5	46.4	207	3.88	.559	13

Names of variables and units (where applicable) are given in the column heads. The variables are as follows. KFIT = carrying capacity, extracted from equation 2.1. RFIT = rate of population growth (r) at low density, extracted from equation 2.1. RTFIT = value of $r\theta$ extracted from equation 2.1, where θ measures the asymmetry of the growth curve. RLH = the rate of increase based on the replacement rate and generation time. REPLLH = the replacement rate, measured from emergence curves (see Fig. 2.1). FSTEMGLH = day of first emergence (see Fig. 2.1). PKEMGLH = day of peak emergence (see Fig. 2.1). LARVPROD = larval production. K-15 = carrying capacity, measured as the number of flies in a single-species system after at least 15 weeks. DRYWT = average dry weight of one fly. COMP = average frequency at the end of pairwise competition with each of the 27 other species; a measure of competitive ability. RANK = competitive rank in Fig. 2.2A (1 = the best competitor, 28 = the worst).

Table 2.3 CORRELATION MATRIX FOR THE PARAMETERS OF TABLE 2.2

	RFIT	RTFIT	RLH	REPLLH	FSTEMGLH	PKEMGLH	MAXEMGLH	LARVPROD	K-15	COMP	RANK
KFIT	−.32	.14	.70	.49	−.22	−.59	.81	.33	.87	.61	−.60
RFIT		−.12	−.13	−.09	−.07	.29	−.18	−.13	−.36	−.21	.20
RTFIT			.00	−.08	−.06	−.19	.05	.04	.19	.16	−.16
RLH				.86	−.14	−.32	.88	.38	.75	.72	−.70
REPLLH					−.11	−.05	.69	.26	.56	.66	.66
FSTEMGLH						.08	−.20	−.22	−.15	−.01	.01
PKEMGLH							−.36	−.09	−.70	−.24	.21
MAXEMGLH								.23	.78	.56	−.55
LARVPROD									.35	.53	−.55
K-15										.68	−.67
COMP											−.99

species studied at both temperatures. The two exceptions were Fun and Gib, which emerged earlier at 19°C, due apparently to a density-dependent effect: greater egg laying leading to denser larval populations, making the medium softer and more digestible. Despite slower development at 19°C, carrying capacities averaged 23 flies higher than at 25°C, though there was much variation among species. For instance, Neb and Paul, both of them tropical species, were respectively about 70% less and 70% more abundant at 19°C than at 25°C. In fact, for every life history measure some species did better at 19°C and some did worse. Thus, the net effect of temperature on *Drosophila* biology is complex.

Pairwise Competition

Results Pairwise competition was studied in all or subsets of our 28 species under five different conditions of temperature and food type (Fig. 2.2). The 10- or 20-species subsets used in Figs. 2.2C–E were chosen from among the middle-ranking competitors of the 28-species thick-food systems (Figs. 2.2A, B).

A first, and important, conclusion is that our results are highly reproducible insofar as the equilibrium state is concerned. It may take more or less time, but a "strong" competitor invariably defeats a "weak" competitor. The overall measure of our concordance between replicates is 88%.

Mathematically, and with our flies in practice, exclusion is an asymptotic process. In some cases we noted that, although no recruits of the "losing" species were being added to the system, two or three of its adults were still present at the end of an experiment (19 weeks), probably because maximal adult survival times in bottles can be on the order of months. We scored such cases as competitive exclusion by the numerically dominant species.

Transitivity The presentation of results in Fig. 2.2 sorts the species such that the most successful tournament competitor (the highest ranking) is listed in the first row and column and so on to the least successful. Clearly, the triangular form of these matrices suggests a dominance hierarchy for all five systems.

There are various ways to quantify hierarchy. The classical method (Landau 1951) was employed in peck order studies of birds. More recently, Petratis (1979) has investigated such measures in an ecological context. However, both of these methods for quantifying hierarchies are based on a binary win-loss outcome. We feel that our results are more properly trinary, win-tie-loss, since there are doubtless true coexistences between pairs. More to the point, we feel it highly artificial to call a numerical 60:40% coexistence as being a win by the species present at 60% frequency, as a binary win-loss scoring would require (cf. Goodman 1979). Arguments against automatically calling the 60% species the winner include the facts that adults of the less abundant species might weigh more; the actual competitive impact on a species is better measured by the depression of its adult numbers below carrying capacity; adult densities are not neces-

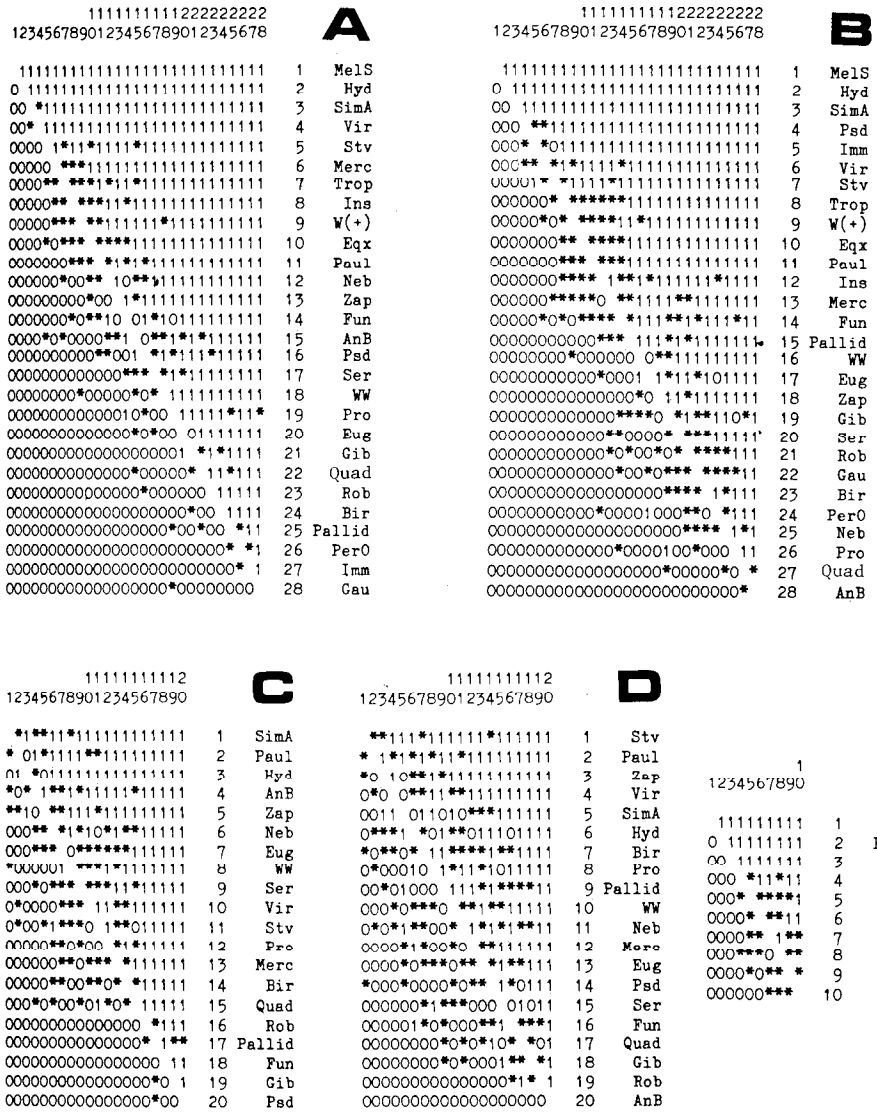

Fig. 2.2 Results from two-species competition trials. A and B are for all 28 species on thick food; C and D are for a subset of 20 species on thin food; E is for 10 species on the augmented system. A, C, and E are at 25°C, while B and D are at 19°C. The abbreviation for the species is given in the right column. Immediately to the left is given the competitive rank of the species (its row number, which is also its column number), from 1 (the best competitor) through 28, 20, or 10 (the worst competitor). A 1 in row "*i*" and column "*j*" indicates that the "*i*th" species excluded the "*j*th" species; a 0 indicates the opposite. For example, in A the 1 in the third column of the second row indicates that Hyd excludes SimA. An asterisk (*) indicates a coexistence or a reversal of outcomes in the replicated trials.

sarily related to larval densities; and the stability of the system may depend on many properties of life history, such that the less frequent species might be the more resilient to disturbance.

Hence, we have decided to employ as a measure of hierarchy one that only counts intransitive exclusions, i.e., the number of 0's that remain in the upper right of the outcome matrix after it has been optimally sorted. For the five systems, the resulting measures of transitivity are:

25° thick food	98%
19° thick food	98%
25° thin food	97%
19° thin food	94%
25° augmented	100%

Thus, as Fig. 2.2 indicates, the degree of competitive transitivity in a given environment is overwhelming.

Shifts of Rank with Environmental Conditions Table 2.4 gives the rank order of the 20 species common to the first four systems, i.e., the thick and thin systems at 25°C and 19°C. The important feature to note about this table is how the rank of some species shifts strikingly with environmental conditions. For instance, with thin-food species AnB is the worst species (rank 20) at 19°C but fourth best at 25°C. Psd has the opposite behavior, going from third best on thick food at 19°C to worst on thin food at 25°C. However, species Quad and SimA retain roughly the same competitive ability (miserable and mighty, respectively) in all four environments. Gause (1934, chap. V) similarly noted shifts in competitive rank of protozoan species with food conditions.

The shifts most susceptible to interpretation are those with temperature. There are 12 cases of species improving and 10 cases of species slipping back by four or more in competitive rank with a shift from 19°C to 25°C (within either the thick-food or thin-food systems). The species that do better at 25°C are drawn disproportionately from the species whose native habitat is the tropics: the pool of 28 species contains 15 tropi-

Table 2.4 COMPETITIVE RANKS OF 20 SPECIES STUDIED UNDER FOUR COMBINATIONS OF TEMPERATURE AND FOOD THICKNESS (FIGS. 2.2A–2.2D)

Species	25°C, thick	19°C, thick	25°C, thin	19°C, thin
AnB	10	20	4	20
Bir	19	16	14	7
Eug	15	11	7	13
Fun	9	8	18	16
Gib	16	13	19	18
Hyd	1	1	3	6
Merc	5	7	13	12
Neb	7	17	6	11
Pallid	20	9	17	9
Paul	6	6	2	2
Pro	14	18	12	8
Psd	11	3	20	14
Quad	17	19	15	17
Rob	18	15	16	19
Ser	12	14	9	15
SimA	2	2	1	5
Stv	4	5	11	1
Vir	3	4	10	4
WW	13	10	8	10
Zap	8	12	5	3

1 = the best competitor; 20 = the worst.

cal and 9 temperate species, but 8 tropical and only 1 temperate species improve at 25°C. Similarly, the species that do better at 19°C are drawn disproportionately from temperate species: 5 temperate and 5 tropical species improve at 19°C.

Also readily interpretable are the shifts in competitive rank between the thick- and thin-food systems at a given temperature. When these shifts were correlated against single-species traits, FSTEMGLH had the highest predictive value: species with later first emergence did comparatively worse in the thin-food system ($p < 0.01$). This is plausible on the grounds that such fly species, when competing against a faster developing species, are more likely to be excluded because they find the limited food supply exhausted before they reach the weight and development limit necessary for pupation.

Prediction of Pairwise Competitive Ability

The last two columns of Table 2.2 give two measures of pairwise competitive ability for each species: RANK, its ranked order of competitive ability in Fig. 2.2A (i.e., on thick food at 25°C), and COMP, its average frequency at the end of pairwise competition with each of the 27 other species. RANK ranges from 1 for the best competitor to 28 for the worst; COMP from 99.7% for the best to 1.4% for the worst. Thus, the correlation coefficient between RANK and COMP is negative (−0.99; Table 2.3).

The signs of the correlation coefficients linking COMP or RANK to the single-species measures indicate that high production and early production promote competitive success (Table 2.3). Thus, larval production (LARVPROD) and all five measures of adult production (MAXEMGLH, REPLLH, RLH, K-15, and KFIT) have positive correlations of 0.53 to 0.72 with COMP. PKEMGLH has a negative correlation with COMP: low values of PKEMGLH promote success because low values mean early production (early peak emergence). Since the best competitor has the lowest value of RANK, coefficients for RANK are virtually the same as those for COMP but with reversed sign.

The origins of competitive ability can be explored further by multiple regression analysis. We multiplied KFIT, K-15, and MAXEMGLH by DRYWT (the weight of an individual fly), thereby obtaining 11 independent variables against which to regress competitive rank. The multiple regression explains 85% of the variance in RANK at 25°C and 65% at 19°C; four independent variables enter with a significant t-value at 25°C, but none does at 19°C. The lower significance of the regression at 19°C may be because fewer replicates were used.

At 25°C four variables, each with a t-value corresponding to $p < 0.01$ or better, explain 80% of the variance in RANK (the other seven variables add only 5%). These variables are the adult production measures RLH, K-15, and MAXEMGLH and the larval production measure LARVPROD. The multiple regression equation is:

$$\text{RANK} = 29.6 - 180\ \text{RLH} - 0.009\ \text{K-15} - 0.14\ \text{LARVPROD} + 0.29\ \text{MAXEMGLH} \quad (2.2)$$

Thus, if a new fly species were added to the tournament, we could accurately predict its rank in pairwise competition on the basis of studying it in isolation. Gause (1934, p. 89) was similarly able to predict the outcome of pairwise competition among yeast species from single-species growth studies.

One detail about equation 2.2 requires comment: the sign for MAXEMGLH. RLH, KFIT, and LARVPROD enter the equation with negative signs and have negative correlations with RANK in Table 2.3 (i.e., large values of these variables tend to yield a RANK nearer to 1 than to 28). However, MAXEMGLH enters the equation with a positive sign even though it too has a negative correlation in Table 2.3. The explanation is suggested by comparing the graphs in Fig. 2.1; species Zap has a low, plateau emergence curve compared to the steeply peaked curve of Psd, and Zap has a correspondingly much lower value of the peak emergence rate MAXEMGLH, yet Zap is a better competitor than Psd. Apparently, the multiple regression is picking up a few such cases and adding their effect as a correction factor to the three other regression variables. A stepwise regression confirms this: MAXEMGLH enters fourth in explaining variance. A mechanistic explanation is that a low MAXEMGLH cou-

pled with a high LARVPROD might indicate that larval activity makes it difficult for pupation to take place; this effect could easily carry over to other species.

Pairwise Coexistence Only 12% of our species pairs (46 out of 378) were able to coexist on thick food at 25°C. When we put 10 species together, we never observed more than 3 species to persist. This result is very different from what happens in nature, where hundreds of *Drosophila* species can coexist in a region. The most important reason for this difference involves the great spatial and temporal heterogeneity of microhabitats in nature, compared to the single such habitat offered in our experiments.

What is it that does permit laboratory coexistence in 12% of our species pairs? There is no tendency for high K and low K species to coexist, for K is highly correlated with competitive ability and the coexisting pairs tend to have very similar competitive abilities, as reflected in the fact that the asterisks [= coexistence] in Fig. 2.2 are clustered about the main diagonal of the outcome matrix. However, when emergence curves (Fig. 2.1) are somewhat arbitrarily classified by shape as either peaked or plateau-shaped, a two-by-two contingency table shows that the coexistences are significantly more common between pairs differing in their emergence pattern. This is quite reasonable and consistent with ideas of production. Species with peaked emergence are better able to exploit the relatively new food in the system, while species with plateau emergence are also able to utilize the food in the older bottles. Thus, coexistence seems to be based on segregation along the niche axis of bottle age.

Assembly Rules

Table 2.5 summarizes the final frequencies (at week 35) of the 30 different trials in which 10 different species were initialized at 30 different sets of frequencies. Examination of Table 2.5 yields five obvious conclusions.

First, the 10-species system always relaxes to a much smaller system: 2 species in 21 trials, 3 species in 7 trials, 1 species in 2 trials, never more than 3 species.

Second, the 10 species differ consistently in how they fared under the 30 different initial conditions. Five species—Ser, WW, Imm, Eug, and Gib—always went extinct regardless of their initial density, which was as high as 91% in 1 trial for each species. Conversely, Paul and Merc almost always survived (in 27 and 25 trials, respectively). Intermediate performers are Neb, Zap, and Psd, which survived in 10, 2, and 1 trials, respectively.

Third, there is close concordance between competitive ability in the 10-species scramble and in the pairwise tournament. From Table 2.5, the descending sequence of survival frequency in the 10-species scramble is Paul > Merc > Neb > Zap > Psd > Ser, WW, Gib, Imm. From Fig. 2.2A and Table 2.2, the sequence in the pairwise tournament is nearly the same: Merc > Paul > Neb > Zap > Psd > Ser > WW > Eug > Gib > Imm.

Fourth, there are assembly rules. Among 10 species, there are $10 \times 9/2 = 45$ possible pairwise combinations, but only 3 of the 45 theoretically possible pairs (Merc-Paul, Merc-Neb, Paul-Neb) ever appeared as a surviving species combination. Of the 21 trials that relaxed to a pair of species, Merc-Paul was the surviving pair in 18 trials. Similarly, there are $10 \times 9 \times 8/6 = 120$ possible species trios, but only 3 of those theoretically possible trios ever appeared as a surviving species combination. Of the 7 trials that relaxed to a trio of species, Merc-Paul-Neb was the trio in 4 trials. Only 2 trials relaxed to a single species, and it was the same species in both cases: Merc. Thus, there are a few permitted or consistently favored species combinations and a much greater number of forbidden combinations. The same pattern was observed for birds of the Bismarck Archipelago and led Diamond (1975) to formulate the concept of assembly rules.

Fifth, these alternative outcomes can in some cases be understood in terms of the starting conditions. Psd, which survived in but one trial (and which probably would eventually have gone extinct there), survived in that trial in which it was initialized at the 91% frequency. It is probably the long survival rates of its adults that accounted for this single case of survival. Zap also survived at a relatively high frequency in the system in

Table 2.5 RESULTS OF COMPETITION AMONG 10 SPECIES INTRODUCED TOGETHER

	Merc	Paul	Neb	Psd	Zap
Corner initializations					
Merc	55	45	0	0	0
Ser	89	0	11	0	0
Zap	0	8	56	0	36
Paul	0	35	65	0	0
Neb	0	5	95	0	0
Ped	0	71	10	19	0
WW	36	64	0	0	0
Imm	66	34	0	0	0
Eug	16	84	0	0	0
Gib	83	17	0	0	0
Broken stick initializations					
(30,15,1,6,5,8,7,13,4,11)	31	69	0	0	0
(8,10,7,6,28,6,1,8,12,14)	74	26	0	0	0
(13,22,9,12,4,7,9,8,11,5)	32	68	0	0	0
(2,7,9,6,3,13,15,22,15,8)	35	65	0	0	0
(4,12,17,11,5,8,3,1,18,21)	55	39	6	0	0
(14,3,8,2,28,4,4,32,4,1)	54	24	22	0	0
(14,2,19,20,3,8,1,2,21,11)	51	49	0	0	0
(33,3,4,3,25,21,2,1,1,1)	100	0	0	0	0
(9,1,28,12,10,4,4,17,5,10)	68	32	0	0	0
(19,4,10,3,3,12,7,13,16,13)	44	44	12	0	0
(8,2,16,6,15,28,20,1,1,3)	24	76	0	0	0
(10,3,36,2,1,20,10,6,6,6)	72	4	24	0	0
(26,11,7,16,7,4,21,3,2,3)	80	20	0	0	0
(20,2,9,11,11,3,10,3,30,1)	0	71	17	0	12
(29,11,12,5,1,6,6,17,8,2)	39	61	0	0	0
(11,26,2,20,4,10,19,4,1,3)	24	76	0	0	0
(2,4,20,1,11,11,7,16,11,17)	21	79	0	0	0
(3,1,5,9,41,16,2,6,12,5)	24	76	0	0	0
(2,1,3,8,37,12,13,9,5,19)	23	77	0	0	0
(9,7,14,8,2,7,22,3,11,17)	100	0	0	0	0

Ten species were introduced simultaneously to bottles of thick food at 25°C. Thirty trials were run, each with a different set of initial frequencies. The trials of the first 10 rows were corner initializations; one species, named at the left of the row (in the first column), was started with 910 individuals, while the other nine species were started with 10 individuals each. The trials of the remaining 20 rows were started with randomly chosen broken stick initializations, given as a vector of percentages at the left of the row, with the 10 species listed in the sequence Merc, Paul, Neb, Psd, Zap, Ser, WW, Imm, Eug, Gib. The numbers in the body of the table are the percentages of the species named in the column heading in the system at the thirty-fifth week. Columns for species Ser, WW, Imm, Eug, and Gib are omitted because those species always went extinct.

which it was started at 91% frequency; it survived in one additional system at 12% frequency and occurred at below 1% in several other systems. Clearly, it is also being excluded; it is simply that exclusion takes longer than the 35 weeks of our experiment. Another instructive example is Merc, one of the two highest-ranking species, which survived in 25 out of 30 trials. In the nine trials where Merc began at 1% and some other species began at 91%, Merc went extinct when the species initialized at 91% was Paul, Neb, Zap, or Psd (the four other highest-ranking species), and Merc survived when the species initialized at 91% was Ser, WW, Imm, Eug, or Gib (the five lowest-ranking species).

CONNECTIONS BETWEEN THE LABORATORY AND THE WORLD

Let us now consider how our laboratory observations relate to the first four issues that we posed at the outset: transitivity of competition, mecha-

nisms of competition, dimensionality, and assembly rules. We shall then conclude with a discussion of the fifth issue, prediction.

Transitivity of Competition

On the issue of transitivity, our laboratory work yielded clear, simple, and illuminating results.

In a homogeneous habitat in the absence of environmental variation, competitive fitness in our 28 *Drosophila* species is highly transitive (94–100% transitive).

At the same time, modest changes in temperature of only 6°C and changes in the thickness or composition of food caused large shifts in the competitive hierarchy (Table 2.4).

Had we been doing our work in the field, against a background of temperature and food type that we could not control, these shifts would have led us to record "intransitivity," but as an artifact. For instance, with thick food but with temperature uncontrolled, Fig. 2.2 yields

Merc beating Paul (at 25°C)

Paul beating Psd (at 25°C)

but Psd beating Merc (at 19°C)

Similarly, at 25°C but with food uncontrolled, Fig. 2.2 yields

Paul beating Hyd (on thin food)

Hyd beating AnB (on thick food)

but AnB beating Paul (on augmented food)

Such shifts of rank due to uncontrolled variables in a spatially heterogeneous environment could lead to field observations of intransitivity. Buss (Chapter 31) documents intransitivity among competing species of sessile marine organisms. However, ours is not the only possible explanation for intransitivity; specific interference is another, and still another applies to the system discussed by Buss.

Mechanisms of Competition

We did not monitor disappearance of resources nor buildup of waste products and other possible allelochemicals with time. We did not systematically study the behavior of individuals. Thus, our evidence about mechanisms underlying the competitive hierarchy that we observed must be inferential. Some indications of the relative importance of exploitation competition, generalized interference, and specific interference are as follows.

Exploitation competition along a single niche dimension would tend to yield a transitive hierarchy of competitive ability. So would generalized interference. Specific interference, however, would tend to yield intransitivity: the outcome of each pairwise contest would depend on the details of the interference that species A happens to practise against species B, rather than on some underlying principle. Since our observed outcomes were so hierarchical, this inclines us to discount specific interference and to favor exploitation and/or generalized interference.

The relative importance of the latter two mechanisms might differ between the thick-food and thin-food systems. In thick-food experiments the food was never used up, hence calories could not have been limiting, but protein might have been.

There is anecdotal evidence for generalized interference under at least some circumstances. The larvae in some cases crowd the entire surface of the food, leaving insufficient space for larvae to breathe or rest. Since larvae do not burrow into the food, only the top layer of food is immediately accessible. After one week the food becomes liquified, and many larvae and eggs drown and are eaten by other larvae. The species Vir (and also Zap) "destroys the habitat" by making the medium soupy and then turning it into a hard, asphaltlike surface. Vir's large and active larval population makes it difficult for larvae of other species to survive. Thus, generalized interference directed at larvae rather than at adults might be important.

On the other hand, 85% of the variance in competitive rank at 25°C could be explained by single-species measures of adult and larval production and carrying capacities. This result is certainly most simply explained by exploitation competition. If competitive rank were instead due mainly to generalized interference such as

habitat degradation, one might have expected superior competitors to have low carrying capacities—the opposite of reality.

Thus, there is suggestive evidence of both exploitation competition and of generalized interference, as Gause (1934, chap. V) also found for competition among protozoan species. Their relative importance requires more study.

Dimensionality

The pattern of pairwise competition that we observed under any given environmental setting was one-dimensional in the sense of Goodman (1979): species' competitive abilities can be arrayed in a single sequence. When competition involved sets of more than two species, only part of this hierarchical structure was preserved, and the outcome became contingent on starting densities. Even in the case of pairwise competitive rank at 25°C, variation in rank was distributed over at least four dimensions: the independent variables of RLH, K-15, MAXEMGLH, and LARVPROD. Thus, community ecologists using the term "dimensionality" need to define their intended use of it carefully.

How can one account for the shifts in competitive rank as the niche dimensions of temperature, food thickness, and food type change (Fig. 2.2)? Under niche theory, each species has a utilization function defined over the dimensions of food thickness, temperature, food type, etc. Normally, competition between species is based on a convolution of these utilizations integrated over the independent axes of the niche space. Such systems permit coexistence where there is sufficient niche separation (the limiting similarity problem). With our system, however, all of the species are evaluated at a single point in the niche space of temperature and food thickness. Thus, competition must be based on the relative rankings of the species at a *point* on the two-dimensional temperature and food-thickness continuum. It should be clear that the relative heights of these utilization surfaces for different species can differ from point to point in such a niche space, yielding changes in competitive rank consistent with these ideas. The cases in which we can most readily interpret these shifts are the improved competitive rank of tropical species at 25°C compared to 19°C and the improved competitive rank of species with early first emergence on thin food compared to thick food. In addition, our analysis of species coexistence indicates still another niche dimension, bottle age; it is along this dimension that coexisting species pairs segregate.

Assembly Rules

Our laboratory results for *Drosophila* species confirm Diamond's (1975) field results for Bismarck bird species: combinations of species drawn from a pool are statistically forbidden or permitted to coexist. The results of both our pairwise systems and our 10-species system fit this pattern. In addition, Diamond found that the presence of a third species could modify or override pairwise rules. This observation opens the door for multiple domains of attraction, since the fate of a species pair depends on the initial composition of the system. Our results also confirm this observation, in that outcome depends on initial frequency (Table 2.5). For instance, the otherwise strong Merc could not succeed at low initial densities against high densities of Paul, Neb, Zap, or Psd.

There are 2^{10} (= 1,024) different possible combinations of 10 species. Our study found 2 to 7 different combinations of species, depending on which states are considered to be transitional and which stable. That is, had the experiment been carried out longer than 35 weeks, it is likely that both Psd and Zap would have gone extinct. The three-species system Merc-Paul-Neb may be unstable and may decay into Merc, Merc-Paul, or Paul-Neb. It is questionable whether Merc-Paul is stable. Regardless, Merc and Paul-Neb are alternative configurations and constitute multiple domains of attraction.

A clue to why outcome depends on initial frequencies is provided by the fate of mighty Merc, highest ranking of the 10 species tested in Table 2.5. Merc survived in 25 out of 30 trials, but went extinct in 5 trials where Merc started at low density (~1%). In these 5 cases Merc yielded to Paul-Neb (plus in 3 cases Psd or Zap, which were

probably in the process of disappearing). It appears that low frequency reduces the rate at which females encounter conspecific males, thereby delaying female insemination, shifting the emergence curve to a later time, and lowering the effective growth rate of the population. Thus, the per capita impact of competitors is not linearly related to density, as the Lotka-Volterra competition equations assume.

OUTLOOK FOR PREDICTIONS

Our goal was to explore the potential power of the community reconstitution approach by synthesizing complex laboratory systems of *Drosophila* flies. We used these systems to study problems of multispecies competition. Our experience yields one type of bad news and two types of good news.

The bad news is that it is difficult to understand the structure even of laboratory communities in which one creates and controls a simple homogenous environment, chooses species, and adds those species singly, pairwise, or in higher combinations at will. After eight years of work we still have not established the relative importance of various proximate mechanisms of competition. We do not have detailed interpretations for why competitive rank shifts with food type. Our understanding of what produces the observed assembly rules is rudimentary. If these tasks are difficult in the laboratory, think how much more difficult they will be in the field, where there is an uncontrolled and heterogeneous environment, dozens or hundreds of relevant but little known species, and no opportunity for studying those species in isolation or in pairs.

One type of good news is that it has proved feasible and rewarding to study a complex laboratory system in steps. Life history parameters of single species can be measured as a function of environmental temperature and food supply; pairwise competition can be reconstructed from those single-species parameters; and the outcome of competition within sets of 10 species is illuminated by the outcome of the pairwise contests. This approach tests whether we really have identified the significant components of a higher system, just as does the approach of a biochemist attempting to reconstitute the mitochondrial electron-transfer system from its components.

The other type of good news is that the laboratory system succeeded in capturing the essence of many phenomena important in field ecology. We were able to confirm unequivocally the existence of assembly rules, competitive exclusion, species coexistence by niche partitioning, competitive transitivity, and one mechanism of competitive intransitivity (i.e., environmental heterogeneity). We were able to predict competitive rank and to interpret some shifts in rank with temperature and food thickness. The richness or multidimensionality of single-species behavior observed in the laboratory accords with *Drosophila* lore (cf. Ayala's [1969] article on the variability of intrinsic growth rate in different environments).

Of the three traditions of experimental ecology—natural, field, and laboratory experiments—the laboratory tradition is the one currently being least exploited. We hope that we have demonstrated the potential value of community reconstitution studies pursued in the laboratory.

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