CHANGING POPULATION STRUCTURE THROUGH THE USE OF COMPOUND CHROMOSOMES

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ABSTRACT

Theoretical calculations and population cage data are presented to illustrate the use of compound chromosomes to change the genetic structure of insect populations.

THERE has recently been a great deal of interest in the use of chromosome rearrangements for the control of insect pest species. It has been suggested (FOSTER *et al.* 1972) that compound chromosomes might be a particularly effective means of genetic control. Theoretically, when normal and compound chromosome-bearing individuals are mixed, the structure of the population will rapidly move away from an unstable equilibrium point toward fixation of one type or the other. The location of the equilibrium point depends on the fitness of the compound strain relative to the normal strain. The purpose of this paper is to show that the experimental results obtained in population cage studies with *Drosophila melanogaster* closely approximate theoretical expectations.

A compound chromosome has two homologous arms attached to a single centromere. Compound chromosomes may be synthesized from a normal pair of chromosomes (a normal chromosome has nonhomologous arms attached to one centromere) by several methods (FOSTER *et al.* 1972; E. B. LEWIS, personal communication). If disjunction of the compound chromosome at meiosis is regular in both the male and female, the maximum fitness of the strain will be 50%. Half of the zygotes formed will be aneuploid, and therefore lethal, while the other half will carry a complete genome (FOSTER *et al.* 1972). Segregation of the compounds in female *D. melanogaster* is regular, but segregation in the male appears to be random; the two nondisjunctive gametes are produced almost as frequently as the two regular gametes (BALDWIN and CHOYNICK 1967). The maximum fitness of a strain of this type is 25%.

A mating between an individual bearing compound chromosomes and a normal individual is sterile because all the zygotes are aneuploid. Therefore, if a population of normal individuals is mixed with a population of compound chromosome-bearing individuals, only two types of offspring result: those from matings of normal $\times$ normal and those from matings of compound $\times$ compound. This situation is formally equivalent to one in which there is complete selection against

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TABLE 1

Theoretical frequencies of normal and compound chromosome-bearing individuals several generations after mixing the 2 types in different proportions

Fitnesses of .25 and .50 (relative to normal—see text) are assigned to the compound chromosome strain

Generation	Release ratio N : CC	Fitness of CC strain	Frequency	
			Normal	Compound chromosomes
1	1 : 1	.25	.8000	.2000
2			.9846	.0154
3			1	0
1	1 : 3	.25	.3077	.6923
2			.4413	.5587
3			.7140	.2860
4			.9615	.0385
5			.9996	.0004
1	1 : 4	.25	.2000	.8000
			Equilibrium point	
1	1 : 6	.25	.1000	.9000
2			.0470	.9530
3			.0097	.9903
4			.0003	.9997
1	1 : 1	.5	.6666	.3333
2			.8889	.1111
3			.9922	.0078
4			1	0
1	1 : 2	.5	.3333	.6666
			Equilibrium point	
1	1 : 3	.5	.1818	.8182
2			.0899	.9101
3			.0191	.9809
4			.0007	.9993
1	1 : 5	.5	.0741	.9259
2			.0126	.9873
3			.0003	.9997

the heterozygote, and the equilibrium for such a population is unstable. If the proportion of compound chromosome-bearing individuals exceeds the unstable equilibrium point, then the compound chromosome strain will move toward fixation. If this proportion is below the unstable equilibrium point, then the normal strain will become fixed.

Table 1 shows expected frequencies of the two types of progeny when normal and compound chromosome-bearing individuals are mixed in various proportions. Fitness of the compound strain is taken to be either .25 or .50, relative to the normal strain. Either strain was considered to be fixed when its frequency went above .9990. If the fitnesses of the three genotypes are taken to be: normal; $NN = 1$, heterozygote; $NC = 0$, compound; $CC = .5$, their frequencies in the population will be p^2 , 0 and $.5 q^2$ respectively. If NN is mixed with CC in a ratio of $1:r$ and mating occurs at random, their frequencies in the next generation will

TABLE 2

Results of competition experiments between a compound second chromosome strain and a wild-type strain (Drosophila melanogaster)

Number of pairs of each strain introduced into the cages are shown below the release ratio

Generation	Original release ratio N : CC	Progeny		Frequency N $\pm$ SE
		Normal	Compound	
1	1 : 1	196	89	68.6 $\pm$ 2.7
2	(40 pairs N: 40 pairs CC)	239	56	81.0 $\pm$ 2.3
3		212	9	95.9 $\pm$ 1.3
4		55	2	96.5 $\pm$ 2.4
5		339	2	99.4 $\pm$.4
6		..	0	100
1	1 : 3	71	159	30.9 $\pm$ 3.0
2	(5 pairs N: 15 pairs CC)	78	197	28.4 $\pm$ 2.7
3		18	226	7.4 $\pm$ 1.7
4		13	156	7.7 $\pm$ 2.0
1	1 : 3 (replicate)	84	167	33.5 $\pm$ 3.0
2	(5 pairs N: 15 pairs CC)	—	—	—
3		—	—	—
4		7	96	6.8 $\pm$ 2.5
5		—	—	—
6		0	..	0
1	1 : 10	5	202	2.4 $\pm$ 1.1
	(2 pairs N: 20 pairs CC)			
1	1 : 10 (replicate)	11	186	5.6 $\pm$ 1.6
	(2 pairs N: 20 pairs CC)			

be $(1/r+1)^2/\text{Total}$ and $(r/r+1)^2 (.5)/\text{Total}$. If the frequency of CC is below the equilibrium value of .67 ($\Delta q = 0$ when $q = 2/3$), then the NN genotype will go to fixation. If the proportion of CC individuals is above the equilibrium point, then the CC genotype will be fixed. The number of generations necessary for fixation depends on the original release ratio. If the release ratio is 1:3 (NN:CC), and the fitness of CC = .5, CC will be virtually fixed in four generations. The unstable equilibrium point for a compound strain with a fitness of .25 occurs at a release ratio of 1:4.

Table 2 presents the results of competition experiments between a strain bearing compound second chromosomes and a wild-type strain (Tokyo). The compound autosome strain was homozygous for the sex-linked mutant yellow; the compound second chromosomes were unmarked. (This strain was checked for the presence of the compound seconds before the experiments were performed by outcrossing to another marked strain of compound seconds.) Three-day-old virgin flies from each strain were introduced into small plastic population cages and allowed to deposit eggs in vials containing cornmeal medium. Table 2 lists the number of pairs of each strain released in each test. Samples were withdrawn each generation for scoring. Experiments were terminated when one or the other type was close to fixation.

The sample sizes in Table 2 are small, partly because a large genetic load is

sustained by the system (in this case the genetic load is proportional to the number of heterozygotes that die each generation).

The experimental results indicate that the behavior of the system is similar to that predicted by the theoretical calculations. The actual fitness of this particular compound strain must be higher than the theoretical maximum of .25, since it is clear that a release ratio of 1:3 is sufficient to fix CC. In the two replicates of a 1:3 release ratio, the frequencies of NN were 7.7% and 6.8% at the fourth generation. One replicate was terminated at this point. In the other, the frequency of NN was 0 by the sixth generation. The fitness of this strain is calculated to be near .35. This higher fitness can be accounted for if the males produce more disjunctional 2L and 2R gametes than nondisjunctional 2L, 2R and 0 gametes. If the males produce 2/3 disjunctional gametes and segregation is regular in the females, the theoretical fitness of the strain would be .33.

At a release ratio of 1:1, the normal strain became fixed, although not quite as rapidly as expected. At a release ratio of 1:10, the frequency of normal flies was below 6% after the first generation.

A strain of compound third chromosomes marked with scarlet and ebony was found to be much less fit than the $\gamma;C(2L),+/C(2R),+$ strain; in this case, the release ratio at which the compound strain was fixed was above 1:6. In another series of experiments with a strain of compound second chromosomes bearing the mutants dumpy and plexus, it was found that the original composition of the population had to be at least 90% compounds for the compound strain to become fixed. Similar observations were made by FOSTER *et al.* (1972) for a compound second chromosome strain carrying the mutant dumpy alone.

These experiments show that it is feasible to use compound chromosome strains as a tool for suppression of insect pest species. For example, compounds could be used to introduce a temperature sensitive lethal into the population. For a complete discussion of the ways in which a compound strain could be used, see FOSTER *et al.* (1972). Cage studies can determine the fitness of each strain to be used and the optimal release ratio for fixation in a small number of generations.

Field studies with *Drosophila melanogaster*, which is a minor pest in tomato fields and wineries, are currently being planned by several laboratories. Hopefully, these studies will expand our knowledge of the population dynamics of compounds and lead to the production and testing of compounds for other more important insect pest species.

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