Israel Journal of Entomology
Vol. XVI (1982) pp. 73-85

FAMILY SELECTION FOR DDT RESISTANCE IN FLOUR BEETLES *(TRIBOLIUM;* TENEBRIONIDAE) AS A MODEL FOR GROUP SELECTION OF FITNESS TRAITS

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ABSTRACT

Five generations of family (group) selection for resistance (R) and susceptibility (S) to DDT in 4 strains of flour beetles *(Tribolium)* did not alter the level of resist- ance materially.

Insecticide resistance measures (LD_{50} or per cent mortality) cannot be taken on individuals and are by definition "populational phenotypes". The present experiment shows that group selection for these characters is no more than an - inefficient, indirect individual selection. It is suggested that processes like those demonstrated in the present work should be described as "selection for a group mean" rather than "group selection".

INTRODUCTION

In human habitats, insects must cope with strong environmental stresses in the form of pesticides. The ability to survive insecticide application becomes a vital fitness trait. Selection of genotypes capable of efficient pesticide detoxification results in insecticide resistance, now a widespread phenomenon (Georghiou and Taylor, 1976), although survival may sometimes be achieved by a change in behaviour (e.g. Trapido, 1952, cited in Brown, 1960;Pinniger, 1974). The genetic basis for insecticide resistance has been confirmed in a number of insects, notably Dipterans (see reviews in Crow, 1957; Brown, 1960;Georghiou, 1969).

Quantitative measurements of insecticide resistance cannot be made on individuals. Per cent mortality, LD_{50} or "resistance factors" (LD_{50} of the resistant strain divided by LD_{50} of a standard susceptible one) are necessarily "populational pheno- types" in the sense of Wade and McCauley (1980). Therefore, these measurements may conveniently be used in experimental studies of genetic changes caused by differential extinction and proliferation of populations (group selection; Wade, 1978 and references therein).

The importance of group selection is a controversial issue in evolutionary biology, partly because scientists who use the term mean different things (review in Wright, 1980). Early workers such as Wright and Haldane dismissed it as unimportant. Wynne- Edwards (1962) argued that it has an important role in the evolution of "altruistic" behaviour, but others disagree (e.g. van Valen, 1971; Zahavi, 1977). The theoretical

models of group selection were recently reviewed by Wade (1978). Wade (1976, 1977, 1979), Wade & McCauley (1980) and McCauley & Wade (1980) renewed the interest in group selection by showing, in experiments with *Tribolium*, that group selection for large and small population sizes, in fact, produced the expected response relative to the unselected control. The authors wished to emphasize that group selection for a populational phenotype is different from individual selection and can be effective in evolution.

The experiment I am about to describe was originally intended to study the response of *Tribolium* populations to family selection (Falconer, 1960), for resistance as well as for susceptibility to DDT. An advantage of family selection in resistance experiments is that the organisms used as parents are not themselves exposed to the poison and, thus, do not suffer any adverse effects on reproduction or competitive ability. The experiment becomes a case of group selection because the family (populational) phenotypes were the criteria for selection of families every generation.

In presenting my data, I wish to illustrate that the success of Wade's experiments resulted from the choice of population size as the characteristic under selection, not from properties of group selection itself, and claim that this form of selection is not different, in principle, from individual selection.

MATERIALS AND METHODS

Family selection for resistance (R) and susceptibility (S) to DDT was carried out for 5 generations in each of four strains of flour beetles: Three *T. castaneum* strains (CS ++, CS bb and CS ss) and one *T. confusum* strain (CF ++). All strains were maintained in a standard environment (30°C, 70% RH) and a standard medium (flour and brewers yeast, 100:5).

DDT was a locally produced commercial product, DIDITIV 50, (Machteshim Ltd., Beer Sheva, Israel), containing 50% active ingredient. In generations 1 and 2 the pesticide was dissolved in water. In generations 3 to 5, it was dissolved in acetone, which gives better and more homogeneously distributed crystals (McIntosh, 1947). Filter paper was immersed in the solution and then allowed to dry for at least 24 hours at room temperature. Control trials proved that exposure to filter paper immersed in either solvent without the pesticide caused no mortality.

Experimental History

Large samples of adults of each strain were taken from the stock jars. Half the beetles of each sample were exposed to 0.3% DIDITIV for 30 min. as described below, and then transferred to empty vials. The survivors were transferred 24 hours later to oviposition jars for the R lines. Simultaneously, the second half of each adult sample was transferred without DDT exposure to oviposition jars for the S lines (Day 0). The reasons for pre-selection of stock adults were: 1) to obtain information on the level of DDT resistance in the stock, and 2) to select quickly a resistant group of founders from each stock. Mortality data from this pre-treatment is not included in the analysis since the age distribution and handling conditions of stock populations are not comparable with the experimental ones.

On day 7 the adults were sifted out and discarded. Pupae were recovered from the jars twice weekly, beginning on day 19, separated by sex and held separate until all became adults on day 35.

Twenty males and twenty females, chosen randomly from each jar, were paired in vials with 5 g of flour and allowed to oviposit for 7 days to produce 20 families for generation 1. The rest of the adults were exposed, in samples of 20, to a series of DDT concentrations (0.075, 0.15, 0.3, 0.6, 1.2 and 2.4% DIDITIV) for measuring the level of resistance of the founding generation (Gen.0).

Selection Procedure

Family selection, based on progeny testing, was practiced four times in 5 experimental generations in 3 strains (6 selection lines). R and S lines were treated identically but for the direction of selection. The fourth strain, CS ss, was discontinued after generation 4 due to very low productivity.

The test procedure was a modification of the standard method for detecting resistance in *Tribolium* (Champ and Campbell-Brown, 1970). Males and females were tested separately. Samples of at least 20, and no more than 40, beetles of each family and sex were exposed to filter paper treated with DDT in standard plastic petri dishes (Wool and Manheim, 1980). The selective doses were 0.3% for the S lines and 1.2% for the R lines.

The dishes were maintained at 25°C during the 24 hour exposure period. The criterion for mortality was "knock-down", defined as the inability of the insect to stand and walk (Champ and Campbell-Brown, 1970).

Four families (occasionally 3 or 5) of the 20 were selected every generation in each line: two families contributing males and two – females. Families showing the lowest mortality in the test samples were selected in the R lines, and those showing the highest mortality – in the S lines. Twenty males and twenty females of the selected families (sibs of the beetles used in the tests) were paired in vials with 5 g of medium, strictly avoiding sib-mating, to produce the next generation, and were discarded after 7 days of oviposition. The remaining offspring from all vials were pooled and tested in samples of 20 on several doses of DDT.

Calculations

In resistance experiments using exposure to treated surfaces, the exact dose of insecticide absorbed by each individual is unknown. Therefore, the parameter LC_{50} (the concentration estimated to cause 50% mortality under the experimental regime) is used for comparisons of resistant and susceptible lines. LC_{50} was estimated by inverse prediction from regression of probit mortality on log dose (Sokal and Rohlf, 1969).

In addition, probit transforms (Y) of all mortality data of each strain (R and S lines combines) were regressed on log dose. Using the slope b of the regression line, each datum Yi was repleaced by the "adjusted" value ($Yi[Adj] = Yi - b[x-\bar{x}]$, where $\bar{x}$ is the mean log dose), to remove the effect of dose on mortality statistically (Sokal and Rohlf, 1969). The resulting variates were listed separately for R and for S and the differences between the two "adjusted" means were tested for significance by t tests.

Per cent mortality, productivity (number of adult offspring per fertile pair) and developmental period (median number of days from oviposition to pupation) were recorded for each family and generation.

The non-parametric sign test (Siegel, 1956) was used for comparisons between R and S lines whenever I did not wish to assume normal distribution of the variable.

Resistance Estimates

In three of the four R lines, LC_{50} increased in the first two generations. The change in procedure then caused a decrease in the estimated LC_{50} in gen. 3. In generations 4 and 5, LC_{50} tended to increase again in 3 of the strains (fig. 1).

LC_{50} in the S lines did not decrease as expected (fig. 1). Still in 14 of the 19 possible comparisons of R and S in the four strains, LC_{50} of R was larger than in S. The probability of this occurring by chance alone is $P = 0.032$ (sign test).

LC_{50}, being a single estimate per line and generation, obscures the variation in mortality within lines. Therefore, I turned to the analysis of (adjusted) mortality. Efficient selection should have reduced mean mortality in the R lines and increased it in S. No such trends were detected (fig. 2). Still in 15 of the 19 comparisons, mean mortality was higher in S than in R (fig. 3, $P = 0.01$, sign test), in ten of them significantly so ($p < 0.05$ to $p < 0.001$, paired comparison t tests). Figure 4 shows the frequency distribution of mortality values of all families in R and S lines. All strains were combined since the shapes of the distributions were very similar. Since males and females of each family were tested independently, the number of samples in fig. 4 is about twice the number of families.

The bimodal distribution of the S and R lines in generations 1-2 resembled the distribution in samples from the stock strains and indicated the presence of variation in resistance, part of which is presumably genetic. In the S lines most families selected as parents – in both stages of the experiment – came from the extreme right hand class (mortality 90-100% on 0.3% DIDITIV). In only a few cases they had to be taken from a family with lower mortality for lack of more suitable males or females. The selected families of the R lines in the early stage were mostly chosen from the extreme left-hand class (mortality 0-10% on 1.2% DIDITIV) although occasional exceptions had to be made. The mortality distribution of the S lines in Gen. 3-5 became skewed in the expected direction – but it is clear that the distribution of the R lines at that period became even more skewed to the left – opposite to the intended direction of selection. The figure illustrates that quite susceptible families had to be chosen as parents for lack of more suitable ones. Family selection was clearly ineffective.

Heritability Estimates

Resistance in *Tribolium* as measured by the filter paper method, is most probably only partially under genetic control. Behavioural factors such as the general vagility of beetles, as well as their physiological state, may affect their fate when exposed to DDT-covered surfaces. As a measure of the genetic contribution to resistance I used the "realized heritability" (cumulative selection gain divided by the cumulative selection differential), $h = (\bar{Y}n - \bar{Y}o)/(\bar{Y}p - \bar{Y}o)$ (where $\bar{Y}n$ is the population mean at gen. n, $\bar{Y}o$ is the initial mean and $\bar{Y}p$ the mean of the selected parents for gen. n).

Table 1 shows two convincing results. (1) In the S lines most of the h values were negative, indicating that mortality was decreasing rather than increasing relative to generation zero (populations became more resistant). Only four of 19 values indicated response in the right direction. (2) The R lines in gen. 1 became more resistant relative

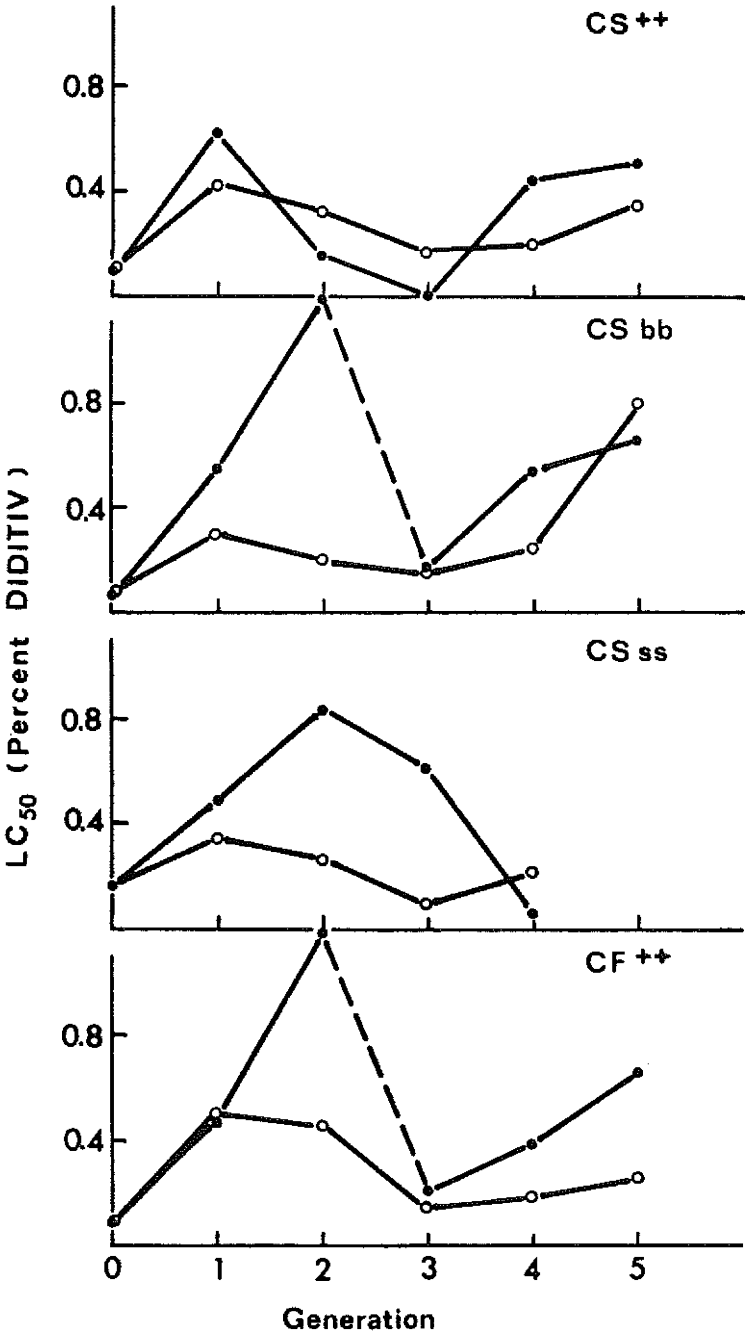

Fig. 1. Changes in LC_{50} in the R and S lines of 4 *Tribolium* strains during five generations of family selection. Dots: R lines, circles: S lines.

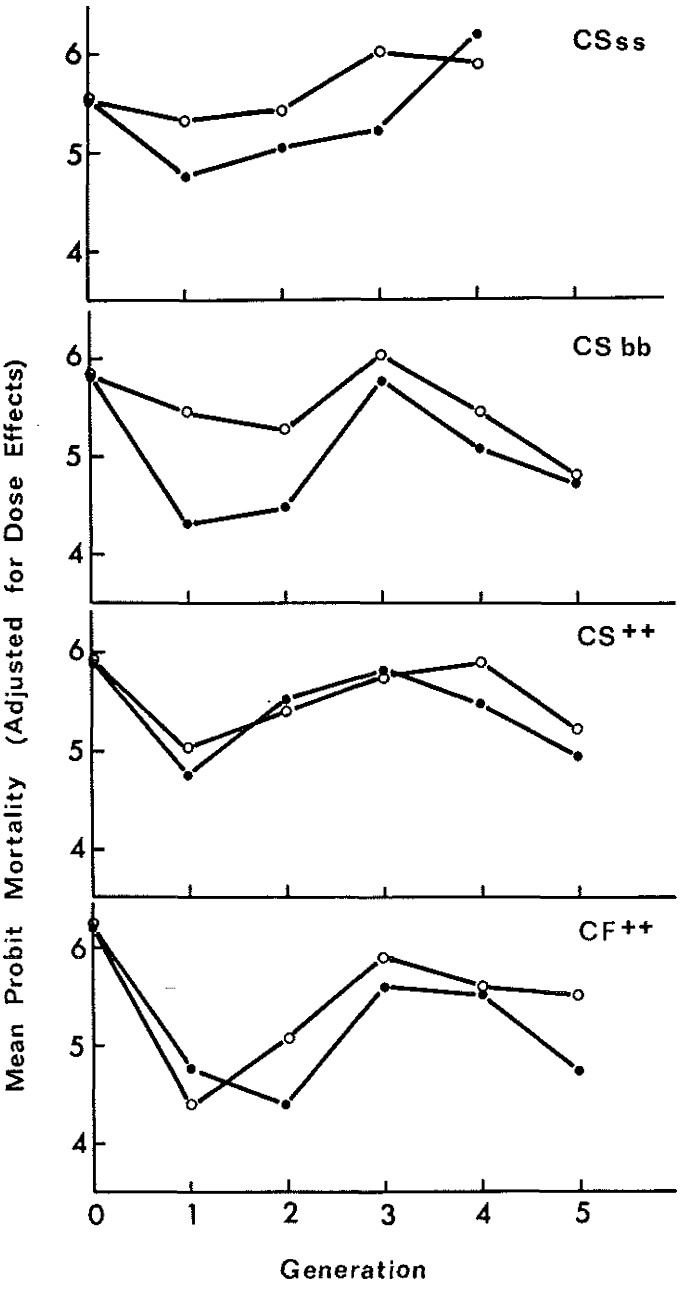

Fig. 2. Changes in mean probit mortality (adjusted for dose effects) in the R and S lines. Note that there is no directional change in the means.

to gen. 0, and mean realized heritability was around 0.4. (But selection which produced this result must have been the direct, individual selection of the founding adults before generation 0). After one generation of family selection h decreased in two lines and increased in one, the mean remaining about the same. Generation 3 and later estimates are not comparable because the change of solvent increased mortality in all lines.

Powell and Lichtenfels (1979) and Wade & McCauley (1980) calculated the realized heritability for each generation from the preceding one $h = (\bar{Y}n - \bar{Y}n\text{-}1)/(\bar{Y}p - \bar{Y}n\text{-}1)$. Part B of table 1 summarizes the h values calculated in this manner from the mortality data, pooled for all generations and strains (R + S). The mean h remained about 0.4 as before, but the response was in the opposite direction in more than half the cases.

TABLE 1. REALIZED HERITABILITY ESTIMATES (ALL STRAINS POOLED).
n = # of lines.

A. Gain relative to generation 0: $h = (\bar{Y}n - \bar{Y}o) / (\bar{Y}p - \bar{Y}o)$

R-Lines

Generation	*mean h*	*range* (n)*	*negative response***	*positive but >1.0***
1	0.426	.303 – .542 (4)	0	0
2	0.395	.144 – .737 (4)	0	0
3	0.128	.014 – .226 (4)	0	0
4	0.764	.750 – .778 (2)	1	1
5	(0.935)	(1)	0	2
S-Lines				
All generations	0.242	.027 – .376 (4)	14	1

B. Gain relative to preceding generation: $h = (\bar{Y}n - \bar{Y}n\text{-}_1) / (\bar{Y}p - \bar{Y}n\text{-}_1)$ (all lines and generations pooled).

mean (± S.E.)	*range* (n)*	*negative** (n)*	*>1** (n)*
0.424 (± 0.0492)	.063 – .827 (15)	(20)	(4)

*only positive values ≤ 1.0 included.
**not included in the range.

Correlated Effects

There were no significant linear trends in either productivity or median developmental time, when tested by regression, except that productivity of CSss R and S lines declined significantly with time. (They were, therefore, discontinued at generation 4).

The variance of productivity and of developmental time among families also did not increase with time. Productivity was the more variable parameter, with the coefficient of variation (CV) ranging from 16% to 45%. Median developmental period was much less variable, with CV ranging from 2% to 6.5%. Both ranges are the same as those measured for our stock strains.

Interestingly, in generation 1, productivity of the S lines was significantly higher and their developmental time was shorter than in the R lines in all strains. The number

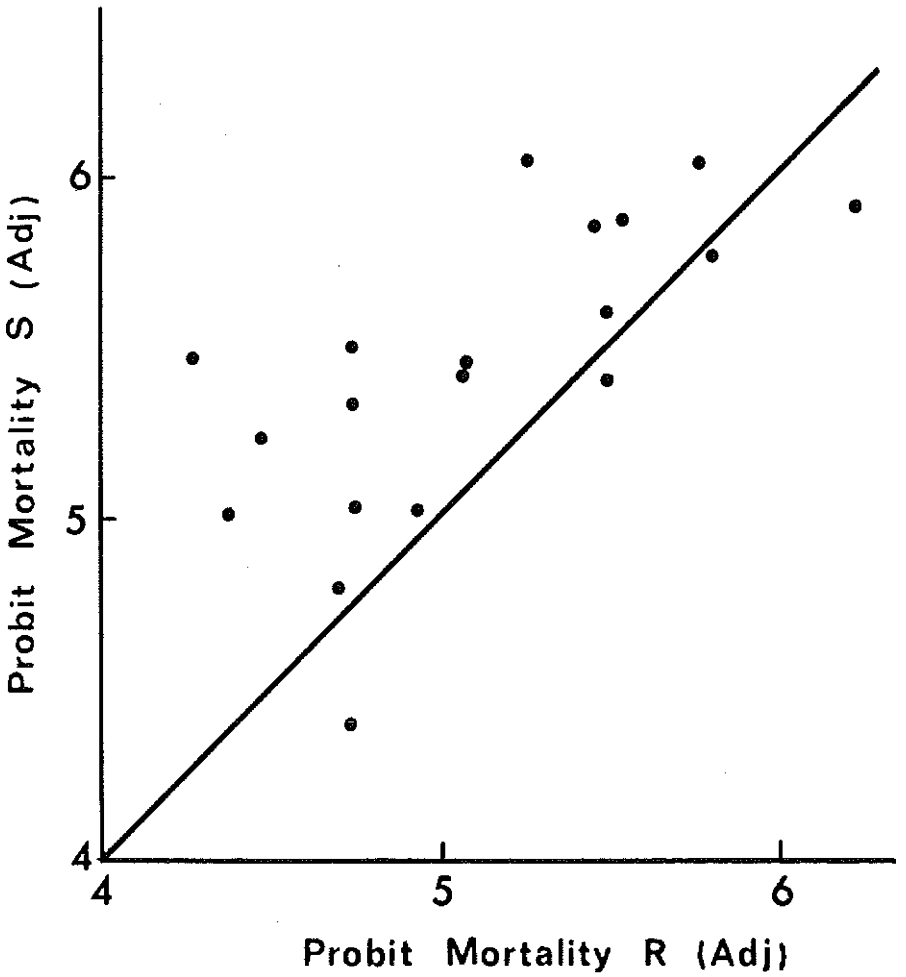

Fig. 3. Comparison of mortality in the R and the S lines. Adjusted probit mortality of each strain and generation is plotted as a single point. The diagonal line represents equal response. In fifteen of 19 comparisons mean mortality in S is higher than in R lines.

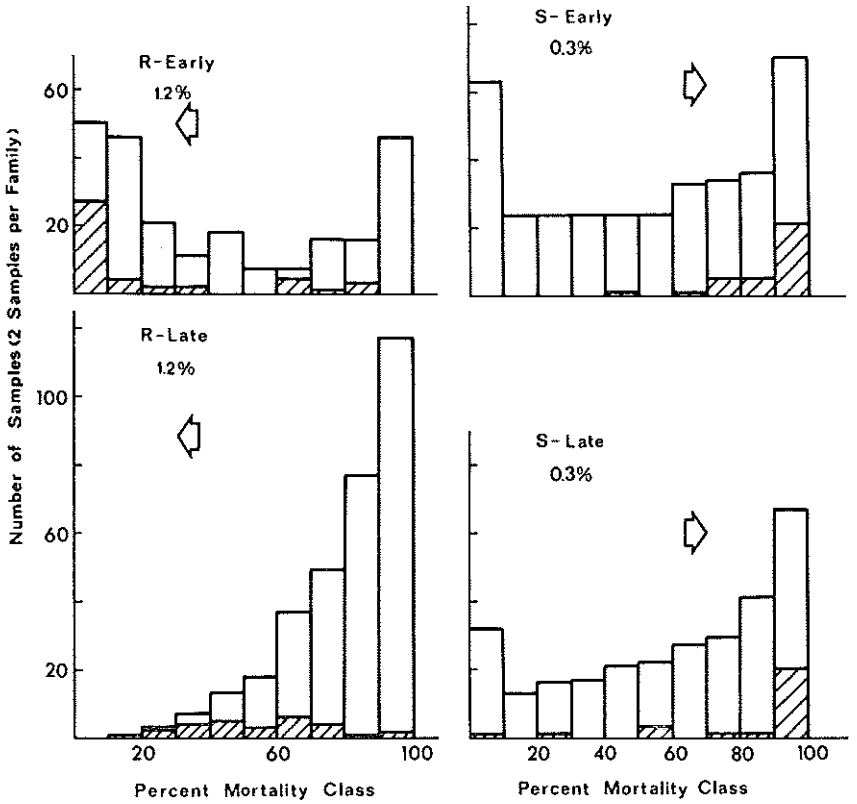

Fig. 4. Frequency distributions of mortality in families of R and of S lines. Most families are represented each generation by two samples – males and females were tested separately. Early (1-2) and late (3-5) generations are plotted separately due to the difference in the solvent of DDT (see text). Black bars indicate those samples chosen as parents for the next generation. Note that in the R lines, the distribution became skewed to the left – contrary to the intended direction of family selection (arrows).

of infertile pairs of parents was considerably higher in R (33.8%) than in S (5%) at gen. 1 (80 pairs in each group). It should be recalled that stock adults which produced eggs for the R lines, were exposed to DDT-impregnated paper for 30 min. The brief period of direct exposure may have impaired the reproductive potential of their offspring. The differences disappeared in later generations.

DISCUSSION

Insecticide resistance in *Tribolium* is well known in different parts of the world (Dyte and Backman, 1970) and some resistance mechanisms were studied in considerable detail (Dyte and Rowlands, 1968; Noiman and Wool, 1982; Wool, Noiman, Manheim and Cohen, 1982). DDT resistance rapidly develops when *Tribolium* individuals are exposed to the poison either by rearing the beetles in DDT-containing flour, or by topical application (Dyte and Blackman, 1967; Erdman, 1966, 1970). It is possible that entirely different genotypes are selected when different methods are applied. This assumption is supported by Dyte and Blackman's line which was further selected by topical application after 8 generations of rearing on medium containing DDT. This line gave, at generation 13, the highest resistance level (X 166) compared to 3 other lines, which were selected only on DDT-containing medium (X 6, X 49 and X 4).

With effective selection, the differences between R and S should have increased with time. In the present study they did not, although selection did maintain the differences in mortality between R and S lines within each strain. Family ("group") selection for resistance was clearly ineffective.

In his experimental study of group selection for large and small population sizes in *Tribolium*, Wade (1976, 1977) found that his selection effectively changed population size in the intended direction. However, Fig. 2 of Wade (1977), in which mean population sizes are plotted, illustrates that selection did not increase population size with time; rather, population sizes of all lines – selected and control – decreased considerably with time. This was attributed to inbreeding depression (see also Wade and McCauley, 1980). It is only relative to the unselected control that group selection was effective, in the sense that size did not decrease as much in High as in Random or Low selection regimes. The differences did increase with time and at gen. 9, the High population produced 40 times more adults than the Low (but in both, less than in gen. 1).

Wade (1977) uses the following definition: "Group selection is defined as that process of genetic change brought about or maintained by the differential extinction and/or proliferation of populations". This definition seems to be acceptable to many authors (see Wade, 1977, 1978 for a review). The experimental procedure in Wade's experiments, as well as in mine, imposed differential extinction and proliferation on the populations, the criterion for selection being a populational phenotype.

Two questions suggest themselves: (1) What are the characteristics of population size and DDT resistance that account for their different response to group selection in the two experiments. (2) Do these experiments demonstrate group selection as a mechanism different from individual selection.

Population size is a much more complex character than per cent mortality. The fixed dimension of the environment for each propagulum in Wade's experiments, and

in particular the fixed amount of food, set an upper limit to population size, and initiated a variety of density-dependent mechanisms limiting population size (Park, 1932; Park, Mertz, Grodzinsky and Prus, 1965). Selection for larger population size – whether done on group means or on individuals – should be opposed by density-dependent mechanisms. Selection for small population size should be free of this limit, but will suffer more from inbreeding depression. The final observed size ("populational phenotype") is the end result of many complex interactions. Incidentally, these mechanisms may create the impression that the individual's reproductive fitness is maximized in the absence of any other individuals, i.e. the "interest" of the individual to produce more offspring is limited by the group – bringing the process closer to Wynne Edwards' (1962) definition of group selection. This is not the case for measures of insecticide resistance.

The two measures of resistance used as criteria in the present work are by definition group characteristics; per cent mortality and LC_{50} indicate the average performance of the family or population, not that of any given individual. One can talk about an individual's probability of survival, but an individual in a group either lives or dies following treatment (the probability of survival assigned to a randomly chosen individual is in fact the proportion of survivors in the group).

LC_{50} and per cent mortality, following insecticide treatment, are density independent. Selection on these characteristics changes the proportion of resistant individuals (genotypes) in the population. Therefore, the results of group selection are readily interpretable.

Group selection, by the definition adopted by Wade (1977, 1978), was practiced in his studies as well as in mine. Defined in this manner, it can easily be understood in terms of partitioning of variance among and within lines in a subdivided population (Slatkin, 1981). If the genetic variation in the character under study is distributed in such a way that group means are rather different from each other, while individuals within groups are rather similar, then selection based on group means will be more effective than selection based on individual values within groups. However, in principle the process is not different from individual selection: selection of large populations is no more than selecting those in which individuals, on the average, are more productive, just as selection of insecticide resistant populations (families) is selection of those populations containing a larger proportion of resistant individuals.

The absence of deleterious changes in fitness characteristics under family selection for DDT resistance in the present study is important in view of the many reports of serious reduction in offspring production and increase in sterility correlated with inbreeding and with individual selection in *Tribolium* (Dawson, 1966; Kress, Enfield and Braskerud, 1972; Wool and Sverdlov, 1976; Wool and Mendlinger, 1981). Also important is the inbreeding depression observed by Wade (1977) and Wade & McCauley (1980). Perhaps, had sib mating been avoided in their studies (as it was in mine), the effects of group selection would have been much less pronounced.

Falconer (1960) used the term "selection for a family (group) mean" to describe selection processes of the form practiced in the *Tribolium* experiments. This term seems preferable to "Group Selection" since the latter term is often used in the literature in the sense of Wynne-Edwards (1962), namely, selection of altruistic traits, advantageous for the group at the disadvantage of the individuals. Whether or not group

selection in the latter definition is a factor in evolution, cannot be resolved by experiments of the type described here, since no such conflict of interests exists in them.

ACKNOWLEDGEMENTS

This study was made possible by the joint efforts of Mrs. A. Tiran and Dr. S. Mendlinger (then a graduate student), who undertook the laborious collection and sexing of thousands of pupae every generation as well as the testing of adults for resistance, and were also responsible for a considerable part of the computations. I am grateful also to Dr. M. Wade, Dr. E. Sverdlov, Dr. Z. Livshits, O. Bergerson, S. Noiman and D. Graur for lively discussions of the results. Finally, thanks are due to an anonymous reviewer of an earlier version of the manuscript, who pointed out some weaknesses in the argument and suggested several changes which improved the final product.

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