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Analysis of genetic control of mating behavior in screwworm (Diptera: Calliphoridae) males through diallel crosses and artificial selection

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Summary. The mode of genetic control of male screwworm (Diptera: Calliphoridae) mating behavior was examined using diallel cross and artificial selection. Diallel crosses showed strong dominance effects, with hybrids being uniformly more successful in copulation than their more inbred parental strains. Weaker additive and reciprocal effects were also noted. Environmental (replicate) effects were highly significant. Regression of array variances and covariances indicated that epistatic interactions or unequal allele distribution during gametogenesis may have occurred and that high courtship propensity polygenes show dominance over low propensity genes. Artificial selection on males from outbred strains from Guatemala and Belize resulted in a decreased number of mating attempts for lines selected for reduced activity, but mating attempts in lines selected for high mating activity did not increase. A combination of inbreeding during the selection cycles as well as selection for recessive traits would explain this response. The two types of experiments were in general agreement, indicating significant dominance and environmental influence on male mating behavior with weaker additive and possible maternal effects.

Key words: Screwworm – *Cochliomyia hominivorax* (Coq.) – Mating genetics – Diallel cross – Directional selection

Introduction

The importance of male mating success as a component determining Darwinian fitness has been established using a number of theoretical and empirical approaches (O'Donald 1980; Rubenstein 1980; Parker 1983; Arnold 1983; Kirkpatrick 1987). Evidence from laboratory experiments and field observations supports the contention that heritable variation in mating behavior exists in many natural populations of insects and that selection operates on this variation (Thornhill and Alcock 1983). Modes of genetic control of mating behavior have been investigated for a few species, including studies of linkage, effects of various mutations, inbreeding, and selection. Experimental determination of the degree of additive genetic variance among strains has been successful for several *Drosophila* species (Fulker 1966; Parsons 1973).

Studies of mating behavior in the screwworm have been carried out in the field and laboratory since the method of eradication by sterile insect release was devised and tested in the early 1950s. The phenomenon of increasing male mating aggressiveness (Baumhover 1965) was demonstrated in laboratory-adapted screwworm strains with asymmetry in mating compatibility between newly colonized and laboratory strains (Crystal and Whitten 1976). An investigation by Mangan (1988) testing hybrids and backcrosses identified two components of mating behavior referred to as aggressiveness (intensity of courtship activity) and selectivity (propensity to attempt mating with laboratory-adapted females). These components were shown to be inherited independently and probably controlled by separate genetic complexes. Mangan (1988) and Hammack (1987) showed that the control of mating behavior was also influenced by complex interactions involving adult age and genetic background as well as environmental factors.

Investigations of genetic control and evolution of mating behavior require methods of dealing with the expression of polygenic systems. As discussed by Carson (1987), genetics has undergone a trend toward increased precision in the study of expression of individual loci and control of specific units of DNA. Studies of polygenes

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and quantitative characters, however, are essential for an understanding of such processes as sexual selection. The classical methods involving the inheritance of polygenes in inverted sections of chromosomes, phenotypic responses to artificial selection, and diallel crosses remain powerful tools for investigating many behavioral traits, including mating behavior (Spiess 1970).

In the present article results from diallel crosses and artificial selection experiments on screwworm lines are presented. The goal of this research was to determine the relative importance of genetic (additive and non-additive) and environmental effects on the reproductive behavior of males. The experimental approach involved crossing and selection processes using strains that had been shown to differ in male mating behavior. These included newly captured isofemale lines, newly constructed strains from reciprocal crosses, and laboratory-adapted strains. The experiments emphasized elucidating the expression of the genetic system controlling mating behavior in males. No effort was made to discover the actual genetic variability for mating behavior in, or among, natural or laboratory populations. The experimental designs used either mating attempts or numbers of matings over a given period of time as indices of mating activity. These measurements will be referred to as mating propensity. Mating aggressiveness will be used to designate level of activity in the sense that it was used in Mangan (1988) or when discussing deleterious effects of aggressive copulatory attempts on female survival. Males attempting to copulate with laboratory-adapted females will be referred to as "responders"; those not attempting copulation with these females will be "non-responders". These terms will be used in place of "selectivity" to distinguish the types of behavior from the artificial selection process.

Materials and methods

Diallel analyses

Two series of diallel crosses were made using newly colonized and laboratory-adapted screwworm strains. Strains were crossed following the same general scheme employed by Fulker (1966). This system analyzed the mating performance of males produced from a matrix of all possible crosses including reciprocals and sib-matings for five strains in experiment 1 (25 crosses) and six strains in experiment 2 (36 crosses). Experiment 1 was replicated three times, experiment 2 was replicated four times. The strains used were derived either from single egg masses (isofemale lines) or from hybridization of 12–16 different lines. Some strains had been maintained under laboratory conditions for less than 1 year; other for more than 10 years. A listing of lines, their pedigree, collection date, and collection location is given in Table 1.

The crossing and testing procedures involved forming a matrix of all possible crosses among n lines, producing n^2 progeny strains. Males from the progeny strains were then placed in cages with two virgin females of each of the parental strains to determine their mating rate. In the first test three males were tested with two females of each of the parental strains for 48 h. For the second test, one male was placed in each cage with two females of each of the parental strains for 24 h. Females were dissected and spermathecae and seminal receptacles were examined for the presence of sperm. In the first test as many as four females died in some cages. Mating success rate in this test was determined as percentage mating for surviving females. In the second test with only one male and shorter male – female interaction time, numbers of inseminated females were used to determine male success rate.

Table 1. Strains used in diallel cross tests

Strain	Type[a]	Collection locality	Collection date
Test 1			
G3101	Isofemale	So. Guatemala	Jan. 1986
B2709	Isofemale	Central Belize	Sept. 1986
V81	Forced cross	So. Veracruz Mexico	Sept. 1981
Sinaloa	Forced cross	Sinoloa, Mexico	Nov. 1979
009	Forced cross	So. Texas	Oct.–July 1974–75
Test 2			
G3101	Isofemale	So. Guatemala	Jan. 1986
CIH34	Isofemale	Colima, Mexico	April 1982
OW87	Forced cross	Central Belize	Sept. 1986
CH85	Forced cross	Quintana Roo, Mexico	Feb. 1985
Sinaloa	Forced cross	Sinaloa, Mexico	Nov. 1979
009	Forced cross	So. Texas	Oct.–July 1974–75

[a] Isofemale = line from a single egg mass collected in the field; forced cross = line contructed by crossing approximately 16 lines

Mating success from the diallel cross matrices was analyzed using the Hayman-Jinks analysis of variance methods (Mather and Jinks 1977). A computer program kindly provided by Drs. D. Z. Skinner and D. L. Stuteville (Skinner and Stuteville 1988) was used to compute the ANOVA tables. Of particular interest in analyzing the diallel data is the regression of the array covariances (W_r) on the array variance (V_r). A mathematical discussion deriving the parameters is given in Dickinson and Jinks (1956). In this analysis the linear regression formula and its significance were calculated as part of the Skinner and Stuteville (1988) program. Interpretations of degree of dominance (or overdominance) ranking of lines according to numbers of dominant alleles, and detection of possible epistasis or unequal distribution of alleles in formation of hybrids was made from the $W_r : V_r$ regression.

Artificial selection

Selection was carried out for six reproductive cycles on males from two strains from Guatemala and Belize. The strain from Guatemala was derived from 16 lines collected as single egg masses from the Pacific coastal plain of Guatemala in January 1986. The strain was constructed by dividing the 16 lines into four groups of 4 lines. Reciprocal crosses were made yielding 12 hybrid lines per group. The 48 hybrid lines were mixed as pupae, and emerging adults were used for the first generation in this test. No intentional selection for rearing characteristics (oviposition, egg eclosion, larval size, pupal emergence) was made.

The OW87 strain was collected in the Orange Walk district of Belize in the Fall of 1986. The original 16 lines were selected from 100 lines based on prompt oviposition, greater than 95% egg eclosion, greater than 65 mg larval weight, and greater than

90% pupal emergence. The strain was constructed by reciprocal crosses of four groups of four isofemale lines each. These hybrids were backcrossed to parental isofemale lines, and the backcross progeny were maintained for two generations. The pupae of the four groups were mixed for the final strain. Second generation adults after the final mixing of the strain were used for the selection experiment.

Selection was carried out on males using propensity to attempt copulation with a laboratory-adapted strain as the selection criterion. For each selection cycle, sexes were separated on day of emergence and maintained in screen cages with honey and water. When males were 4 or 5 days old (5 days when laboratory temperature fell below 22 °C), each male was placed individually in 6-dram vials with a single, 5-day-old, female from the 009 strain. This was the most laboratory-adapted strain available (Mangan 1988). Males attempting to mate with the 009 females during a 2-h observation period were designated "responders", while those not attempting to mate were designated "non-responders". All males of each type were placed in separate cages, and their virgin female siblings were introduced immediately. After 5 days, females were allowed to oviposit and offspring were reared for the following selection cycle. The selection cycle involved four replicates (experiment 1) and six replicates (experiment 2). Replicates were initiated in a single day for both experiments.

After initiation, selection cycles were continued in a similar manner with sexes separated at day of emergence and 100 males tested for 2 h. However, only males attempting to mate were saved in the responder group, and only inactive males were saved in the non-responder group. Males were then placed with virgin females of their respective selection lines. For each selection cycle, two replicates were tested per day over a 3-day period. Two replicates were tested in the morning (ca. 7:30–9:30 am) and two at about mid-day (ca. 10:30 am–12:30 pm). Responders and non-responders from the same replicate were always tested at the same time. It should be noted that selection was only carried out on males of the lines and the 009 strain females were only used as testers, no genetic material from the 009 line entered the genomes of the lines being tested. The selection process involved three treatments: no selection but possible stress from laboratory adaptation (generation 1); selection for attempted mating with 009 (responders); selection for not attempting to mate with 009 females (non-responders). The latter two treatments were applied after generation 1.

Data recorded included numbers of mating attempts per male, numbers of males attempting to mate at least once, and numbers of males mating. Analyses were carried out on the mating attempt data for effects of replicates, selection regimes and selection cycles on level of activity. Numbers of mating attempts for 100 males in 2 h were recorded for analysis. Analyses of covariance (Sokal and Rohlf 1981), with generation as the covariate and lines and selection as discrete treatments, were performed using the MGLH module of the SYSTAT statistical package (Wilkinson 1988).

Results

Diallel crosses

Strains can be classified by number of generations in the laboratory as old (009, Sinaloa, V81, CIH34) and new (G3101, B2709, OW87, CH85), by pedigree (isofemale, composite), and by geographic origin (northern Mexico and Texas, southern Mexico, and Central America). Experiment 1 was originally designed to include seven lines (those given plus OW87 and a line from Oaxaca, Mexico). Crosses involving the Oaxaca and OW87 failed to oviposit in several replicates. All crosses involving these lines were omitted from the analysis in experiment 1. Experiments 1 and 2 share similar designs and several strains; they differ in some strains, in numbers of replicates (3 versus 4), in numbers of males tested per cross (3 versus 1), and in time for crosses (48 h versus 24 h). In addition, the experience of performing experiment 1 greatly improved handling of crosses for experiment 2 and probably reduced experimental error due to stress on the flies.

In Table 2 performances of males from hybrid and inbred strains are given. Each hybrid performance is the mean of all hybrids formed for which the given line served as the maternal or paternal parent. Each insemination rate in experiment 1 is, therefore, the mean of 4 hybrids replicated 3 times, while each rate in experiment 2 is the mean of 5 hybrids replicated four times. Insemination rates for inbred males were also replicated three times in experiment 1 and four times in experiment 2.

In both experiments (Table 2) hybrid males were more successful than inbred males in inseminating females. When the reciprocals were averaged, hybrids were more successful than inbreds for all strains. When the reciprocal columns were treated separately, only hybrids involving 009 males in experiment 2 were less successful that the inbred 009 strain. The inbred 009 strain had the highest insemination rate of any of the inbred strains in both experiments.

Values for the variance of the array for each parent (V_r) and the covariance of each array with the inbred parent (W_r) are given at the bottom of Table 2. Lines having the lowest points on the plot have the most dominant alleles (Mather and Jinks 1977); in this case, 009 and Sinaloa for experiment 1 and 009 and OW87 for experiment 2 were lowest. The regression of V_r on W_r was not significant, however, indicating that other non-additive effects in addition to dominance were affecting mating rate.

Table 3 gives ANOVA results for the diallel experiments. In these tables there are two main effects: genotypes and replicates. The MS (mean squares) for these effects correspond to the genetic variance and environmental variance contributions to the total variance in numbers of matings. Genetic variance is then broken down into crosses (each combination of lines making up hybrids), selfs (the inbred lines), and crosses versus selfs (dominance or heterotic effects). Crosses variance effects are associated with additive variance. At the bottom of the ANOVA a separate "reciprocal" variance (due to asymmetry in reciprocal crosses) is given.

In both experiments environmental effects (replicates) and cross versus self were highly significant. This agrees with the analysis in Table 2 showing that for all

Table 2 A, B. **A** Mean percentage of females inseminated (Expt. 1) and mean number of females inseminated (Expt. 2) for hybrid males with common paternal and maternal lines and for inbred strains of males tested with females of each of the lines. **B** Variances of individual arrays and covariances of each array with the parental (inbred) array

A

	Experiment 1				Experiment 2		
Line	Hybrid Paternal	Hybrid Maternal	Inbred Line	Line	Hybrid Paternal	Hybrid Maternal	Inbred Line
G3101	77.7	74.2	69.8	G3101	1.8	2.2	1.0
009	85.6	79.8	75.7	009	3.3	1.7	2.0
Sinaloa	82.2	86.0	72.8	Sinaloa	1.6	2.9	0.8
B2709	82.0	79.6	73.0	CIH34	2.4	2.1	0.8
V81	75.8	83.8	66.6	CH85	2.3	3.1	1.5
				OW87	2.2	2.5	1.8

B

Line	Variance (V_r)	Covariance (W_r)	Line	Variance (V_r)	Covariance (W_r)
G3101	2.685	10.571	G3101	0.3109	0.2344
009	20.710	−20.781	009	0.4167	−0.2958
Sinaloa	47.706	−19.244	Sinaloa	0.8339	0.2948
B2709	89.814	46.239	CIH34	0.6125	0.3000
V81	109.892	34.008	CH85	0.5104	0.1292
			OW87	0.4813	−0.0500
regression b = 0.594, a = −16.608			regression b = 0.602, a = −0.118		
$t = 2.19$, $df = 3$, $P > 0.10$			$t = 1.04$, $df = 4$, $P > 0.10$		

Table 3. Anova table for diallel cross experiments 1 and 2

Experiment 1					
Source	*df*	SS	MS	*F*	*P*
Genotypes	24	6,582.16	274.26	1.72	0.055
Crosses	19	4,758.69	250.46	1.57	0.104
Selfs	4	302.79	75.69	0.46	0.754
Cross vs. self	1	1,520.68	1,520.68	9.54	0.003
Replicates	2	2,546.44	1,273.22	7.99	0.001
Error	48	7,650.25	159.38		
Total	74	16,778.84			
Reciprocals	10	2,521.31	252.13	1.58	0.140
Experiment 2					
Source	*df*	SS	MS	*F*	*P*
Genotypes	35	142.69	4.08	1.94	0.005
Crosses	29	117.97	1.14	1.93	0.008
Selfs	5	5.71	1.14	0.54	0.744
Cross vs. self	1	19.01	19.02	9.02	0.003
Replicates	3	55.52	18.51	8.78	<0.001
Error	105	221.23	2.11		
Total	143	419.44			
Reciprocals	15	73.75	4.92	2.33	0.006

lines, hybrids were superior to inbred crosses in mating rate. The two experiments were also in agreement in showing that selfs, the effect of the inbred lines, were non-significant. Experiments 1 and 2 differed in the effects of crosses and the effects of reciprocals. This led to differences in overall genotype effects for the two experiments. When the effects are ranked according to significance, the two experiments are in agreement, replicates being more significant than genetic effects and crosses versus self > crosses > selfs for the genetic effects.

Selection experiments

Numbers of mating attempts (strikes) per 100 males are plotted in Fig. 1 for the Guatemala and Belize selection experiment. The experiments were designed to continue for six generations. Several lines failed to oviposit during the Belize experiment and had to be discontinued. This failure appeared to be caused by stress on the females from male mating aggressiveness. This was rectified in the Guatemala experiment by using 200 Guatemala females for breeding to the selected males and by removing males from cages when female mortality was evident.

For both the Guatemala and Belize experiments, by generation three or four the non-responder lines had reduced numbers of mating attempts and variability among lines. Responder lines were highly variable in

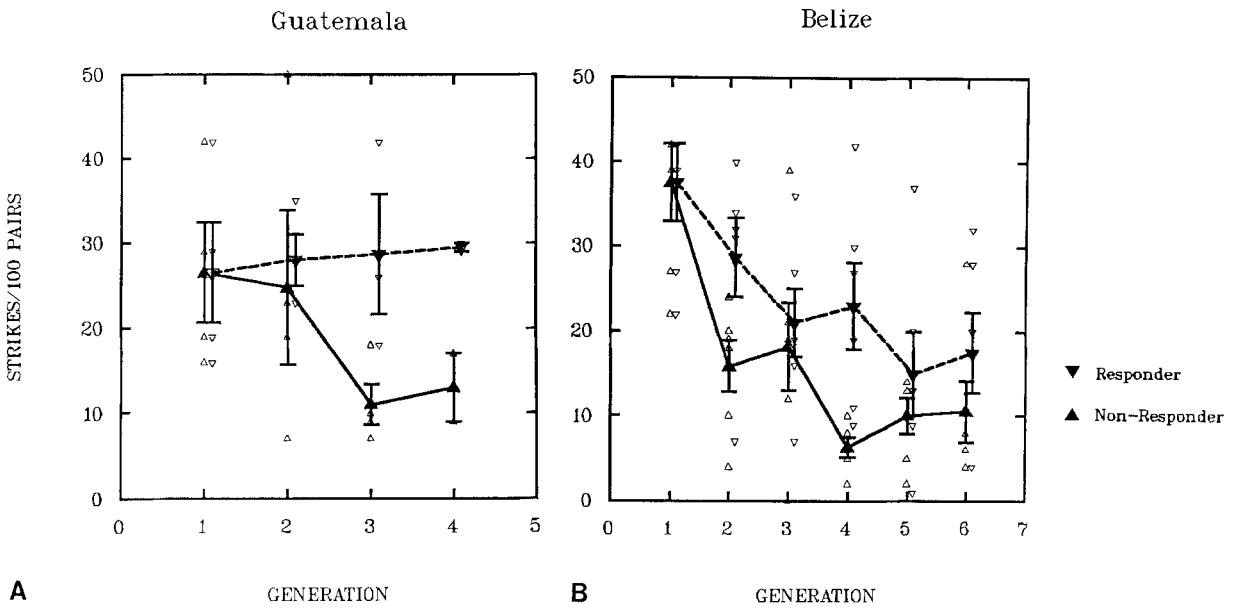

Fig. 1 A, B. Responses of male courtship attempts (strikes) to selection for outbred lines from Guatemala (**A**) and Belize (**B**). Responders were lines in which only males attempting to male with a females from a reference line were kept; non-responders were lines in which only non-active males were kept. *Bars* represent standard errors; *triangles* represent performances of individual lines

Table 4. Analysis of covariance tables for male mating selection experiments 1 and 2. Generation (gen) is analyzed as a covariate with line and selection (sel) as discrete source variables

Experiment 1. (4 Guatemala lines, 4 generations)					
Source	*df*	SS	MS	*F*	*P*
Line	3	1.073	0.358	2.012	0.153
Sel	2	1.892	0.946	5.318	0.017
Gen	1	0.237	1.330	1.330	0.266
Error	16	2.846	0.178		
Experiment 2 (6 Belize lines, 6 generations)					
Source	*df*	SS	MS	*F*	*P*
Line	5	5.651	1.130	3.007	0.018
Sel	2	7.230	3.615	9.618	<0.001
Gen	1	1.973	1.973	5.249	0.026
Error	57	21.432	0.376		
Experiment 2 (6 Belize lines, omit generation 1)					
Source	*df*	SS	MS	*F*	*P*
Line	5	6.310	1.262	3.238	0.013
Sel	1	5.940	5.940	15.238	<0.001
Gen	1	1.973	1.973	5.062	0.029
Error	52	20.270	0.390		

both experiments, but there was no evidence for an increase in mating attempts in either experiment. Analysis of the effects of selection, lines and generation on numbers of strikes is given in Table 4 for both experiments. In addition to the two selection regimes for mating propensity and adaptation there was considerable inbreeding, especially from generation one to two when the maximally outbred populations reproduced. Generally, 5–30 females oviposited each generation, but in each of the lines in both experiments as few as 3 females oviposited at least once during the first three generations.

Further analyses of generation effects were made for the Belize experiment by using only data for generations two through six. The ANOVA for this portion of the data showed generally the same trend: the selection regime (Sel) still had the greatest effect, while generation and line were significant. This analysis indicated that while inbreeding may have been associated with changes in mating activity between generations one and two, differences between the selection regimes continued in following generations.

Discussion

In this study the agreement of results from diallel crosses and artificial selection suggests a mode of genetic control of mating behavior of srewworm males. Results from the diallel tests indicated that the strongest genetic effect detected was the dominance effect, with high mating propensity showing dominance over low propensity. Weaker additive and reciprocal genetic effects were also found in the second diallel experiment. Weak additive effects and a decline in mating propensity which could be explained by loss of heterosis were also indicated by the

selection experiments. Outcrossed lines selected for increased response to laboratory-adapted females did not respond, lines selected for decreased responses showed significant decrease in mating activity as would be expected if low mating propensity (with lab-adapted females) were recessive, and a large portion of the population was heterozygous. The decline in mating propensity in both lines during the Belize selection experiment indicates that additive genetic effects alone cannot explain control of mating propensity. In both diallel and selection experiments the effects of environmental variance were considerable.

The validity of these interpretations from the diallel results depends on certain assumptions as well as on certain underlying principles from quantitative genetics. Diallel analysis requires several conditions for an accurate evaluation of results. The parental lines must be inbred or there must be an unbiased distribution of alleles in gametes and production of hybrids (Dickinson and Jinks 1956). Violation of this assumption can result in non-significance of the regression of V_r on W_r, and evidence for other non-additive genetic effects become confounded with gene distributions during hybrid formation. Most of the lines were more inbred than wild populations, as they were isofemale lines which had been maintained under conditions allowing 3–10 females to reproduce each generation, or which had been maintained for hundreds of generations as small (<20 reproductive females) populations.

Two of the lines, CH85 and OW87, were recently colonized, outbred lines, and could have been heterozygous at some important loci. If CH85 and OW87 were showing bias in gametogenesis, their array variances (V_r) should have been greater than the more inbred lines. In fact, these lines ranked third and fourth (Table 2B) in array variance size of the six lines in experiment 2. In both experiments, old lines (V81 in experiment 1 and Sinaloa in experiment 2) had greatest array variances. This does not preclude the possibility suggested by Carson (1987) that even very old laboratory stocks may have considerable heterozygosity. Very low levels of heterozygosity have been reported (Dev et al. 1986; LaChance and Whitten 1986; Snow et al. 1985, Roehrdanz and Johnson 1988) for natural and laboratory screwworm populations in general for polytene and karyotype chromosome studies, for electrophoretic variation, and for mitochondrial DNA. Mangan (1988) showed that four laboratory-adapted strains including 008, V81 and Sinaloa (studied here) showed similar behavior patterns but variation in mating success when tested with newly collected lines.

Alternative causes of non-significance of the regression at the bottom of Table 2B include epistasis between or among loci and reciprocal effects. Deviation of the regression lines from unit slope (b=1) was probably caused by the overdominance which was shown in Table 2A and the ANOVA's in Table 3.

Differences between diallel experiments 1 and 2 are largely due to differences in the relative magnitude of the error term (Table 3). Since the first experiment used three males to test each line and the second used only one male, contagious behavior (all males becoming active if one attempts mating) may have increased the variance among mating tests in a random manner. In addition, the longer mating period would increase the chance that recalcitrant females would yield to mating attempts or suffer increased mortality. In the two experiments differences in the lines used may also have affected relative mating rates (Table 2).

The overall results of these diallel tests differ somewhat from those reported by Parsons (1964) and Fulker (1966) for *D. melanogaster*, and by Parsons and Kaul (1966) for *D. pseudoobscura*. Those investigators studied mating rate in diallel analyses very similar to this study, but they reported extensive additive genetic effects as well as significant dominance effects. They reported no evidence for epistasis or reciprocal effects, and they had no significant replicate effects. Parsons (1973) cites a number of studies in *Drosophila* which have shown strong additive and dominance effects for mating rates. The presence of very strong dominance and heterotic effects in dipteran mating systems has also been discussed in a number of studies mainly focused on *Drosophila* (Carson 1987).

The analysis of screwworm male mating behavior and that for *Drosophila* differed most drastically in the replicate (=environmental) effects. This suggests that the extrapolations for interpreting genetic structure of wild populations would be tenuous since differences between laboratory and natural environments are greater than among replicates in the same laboratory. The results may, however, prove valuable in predicting genetic structure and rates of change in mass rearing populations used in eradication programs. Several factors are notable in the selection experiments. First, in comparison with Mangan (1988), the strains tested in these experiments averaged 26.5 (SD=11.7) (experiment 1) and 37.5 (SD=11.3) (experiment 2) strikes per 100 pairs in 2 h; new isofemale lines in Mangan (1988) averaged 15.0 (SD=14.6) strikes per 100 pairs per 2 h. The 009 line males in Mangan (1988) tested with new line females, however, averaged 353.3 (SD=264.2) strikes per hundred pairs per 2 hours. New line males from the isofemale lines appear to have about half the mating propensity of outbred new lines when tested with old line females. Outbred new line males were only one-tenth as aggressive with the 009 females as the 009 males tested with new line females.

In the analysis of variance (Table 4) differences between experiments can be associated with differences in

design and execution. Experiment 1 had fewer lines (replicates), was carried out for fewer generations, and because of termination of lines at different generations, was unbalanced. Despite these differences, the two experiments ranked the effects in the same order of significance. The nearly identical results for Belize lines analyzed with and without generation one suggests that the laboratory adaptation processes were not significant factors in the responses of the lines to selection.

While the overall response to selection (Fig. 1) was not very strong and there was a great deal of variance among the lines, the divergence was significant. Experiments selecting for mating speed on male *D. melanogaster* did not result in significant divergence (Manning 1963). Gromko and Newport (1988) similarly showed no response to selection when *D. melanogaster* males were selected for fast or slow remating speed, and a father-son analysis of a series of quantifiable mating characteristics showed significant heritability only for copulation duration (Gromko 1987). Speiss (1970) in a review of extensive selection and analysis literature on *Drosophila* mating behavior concluded that when both males and females are selected for mating speed, changes in female vigor (reduced in fast mating lines) accounts for most of the genetic change. Males in fast mating lines had increased vigor in comparison with controls.

An understanding of the control of male mating behavior in screwworms requires more than just a statistical allocation of variance effects. The mechanism of the dominance effects (number of loci and alleles, linkages and mechanism of expression) and identification of the environmental factors influencing mating behavior must be determined in order to fully describe the genetic control of this behavior. Environmental factors, especially those related to ontogeny of female pheromone production in both adult and larval environments, are likely to prove important in explaining the environmental effects found in these experiments. Hammack (1987) has shown that laboratory-adapted (old line) females become maximally stimulatory at an earlier age than newly colonized lines. It is likely that such factors as temperature and larval diet also influence pheromone production.

The strains used here differed in degree of laboratory adaptation. The line having the greatest consistent success in both tests described here and in Mangan (1988) was the 009 strain, which (Table 1) has been reared under laboratory conditions the longest. It was contended in Mangan (1985) that lack of mate selectivity for males of a species such as the screwworm with populations making up a minute portion of the total muscoid community in tropical habitats would be highly detrimental to mating success. Strains have been changed in the screwworm production facility at regular intervals (1–3 years) for the last 20 years to avoid alleged effects of strain deterioration. However, as of 1990, no field test has been executed to show that a laboratory-adapted strains is inferior to a newly colonized strain in mating success with wild females.

These experiments provide necessary information for constructing strains if optimal phenotypes for reared, sterilized, and released males were known. Weak additive heritability and maternal effects and much stronger dominance effects contribute the major part of genetic control. Decisions concerning selection regimes, criteria for selection of genetic material, and crossing schemes should be based on the knowledge that propensity to mate with laboratory-adapted females and overall vigor of mating activity are independently inherited and show additive dominance over male courtship behavior not requiring cuticular pheromones and less aggressive courtship (Hammack 1986; Mangan 1988). Mating speed, which appears to be controlled by an interaction of selectivity and aggressiveness (and possibly other traits), showed highly significant overdominance and weak additive and maternal effects. The highly significant environmental effects suggest that tests to compare candidate lines for inclusion in a strain should be made under identical rearing and testing ambient conditions.

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