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Selection for mating propensity in irradiated populations of the cotton boll weevil

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Summary. Twelve generations of family selection for 10-day post-irradiation male mating propensity resulted in significant divergence between the selected and unselected control populations. Much of this divergence was the result of a decline in the control population which was believed to have been a function of both inbreeding and environmental effects. Significant correlated responses as measured by differences in the two populations for linear time trends of performance on generations of selection were observed for 10-day post-irradiation survival, percent survivors mating at 10 days, and 7-day egg production of unirradiated females.

Key words: Boll weevil – Mating propensity – Irradiation – Selection

Introduction

In 1979 a project was initiated to develop a laboratory strain of the cotton boll weevil that could be used as a mass release strain in either a pest management or eradication program. Under the assumption that radiation would continue to be used as a sterilization tool, our first efforts were aimed at developing a line that could better withstand the debilitating effects of irradiation. A selection experiment for 14-day post-irradiation survival produced quite dramatic results in increasing the length of time individuals could survive following exposure to high doses of radiation. (Enfield et al. 1981, 1983). For the laboratory strain to be effective in the field, it not only was important that the males survive longer, but also that they actively mate with the wild population. Given our success at increasing longevity, we decided to investigate whether selection could also be effective in increasing the fraction of males that would mate several days after irradiation. Our most recent effort, described in this paper, was a selection experiment for 10-day post-irradiation male mating propensity.

Materials and methods

The selection experiment was initiated from a foundation line that was established from the population originally selected for 14-day post-irradiation survival and the unselected control population from that same experiment in the following way: the two populations were crossed to produce an F_1 followed by one generation of backcrossing to the selected population. The goal was to have a foundation population that was highly resistant to irradiation but where there was some genetic variation for resistance. Results from our earlier experiment indicated that selection may have been effective in exhausting additive genetic variance for 14-day post-irradiation survival. One of our interests was to determine whether genes which might respond to selection for mating propensity were the same or different than those which provided the additional longevity from selection for post-irradiation survival.

As in the previous experiment, family selection was employed. The criterion for selection was the fraction of males from a full-sib family that mated at 10 days post-irradiation out of all males originally irradiated in the family. A Select and Control population were established from the same foundation material and maintained at the same effective population size throughout the experiment so that any effects of inbreeding due to finite population size would be the same in the two populations. In the Select population, unirradiated males and females were used for breeding to produce the next generation from those families having the highest male mating propensity. In the concurrent Control population, the families were chosen at random. In both populations, 18 males were each mated to 2 females each generation, which under perfect conditions would provide data on 36 full-sib families. Each female was allowed to oviposit for 7 days with the eggs collected daily. Eggs were placed on larval diet daily. Records were kept on egg produc-

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tion, number of larvae, and pupae produced, and adult emergence.

Ten males from each full-sib family were irradiated at 2 days post-emergence with 10,000 rads of $_{60}$Co gamma rays. These males were not fed until after irradiation. Leopold (1986) showed that delaying feeding until after irradiation increased longevity. In a limited number of families, less than 10 males werre irradiated due to small family size. The minimum criterion for data collection was that at least five males in a family were irradiated. Rearing procedures were essentially those of Earle et al. (1970). All adult individuals were fed on paraffin-coated diet plugs and were moved to clean one ounce cups every second day.

The mating propensity testing was done according to the following procedure: each male was placed in a cup with an unirradiated virgin female on the 10th day following irradiation. Virgin tester females were obtained from the original control population of the radiation resistance experiment. Each pair was observed for 1 h. Successful mating was defined as the pair remaining in copulation for at least a 15 min period. A seperate study measuring sperm transfer has indicated that about 85% of the males that are observed in copulation for this period will also transfer sperm.

In the Select population, unirradiated individuals (both males and females) were saved for breeding to produce the next generation from the families which had the highest fraction of irradiated males mating. It should be noted that the criterion is really composed of two components. The individuals must first survive the effects of irradiation for 10 days and then must be capable of mating. Records were kept from each family on the number of males that survived and also the number of survivors that mated. The same number of families werre saved in the Control and Select populations each generation so that any effects of inbreeding (and/or population size) would be the same in the two populations. Full and half-sib matings were avoided. In most generations, six females and three males from each of six families were used to produce the next generation. Thus, the fraction of families selected was one out of six in nearly every case. The average selection differential each generation was approximately 22; i.e., mating propensities of males in the selected families were 22% above the mean of all families in the Select population for that generation.

Results and discussion

The direct and correlated response to selection for the three primary traits of interest are shown graphically in Figs. 1–3. A generation 12 comparison of the Select and Control populations for all traits on which data were collected is given in Table 1. Time trends as measured by linear regression coefficients for all traits of interest in the Select and Control populations are summarized in Table 2.

Table 1. Mean comparisons of the select and control populations in generation 12

Trait	Select population	Control population
Mating propensity	54.5±3.9[a]	12.7±3.0
% Survivors mating	55.6±3.9	17.3±4.1
10-day post-irradiation survival	98.0±0.9	69.9±6.0
7-day egg production	78.0±7.5	50.8±6.6
Egg-adult survival	46.8±2.9	48.5±3.8
14-day post-irradiation survival[b]	70.4	5.7

[a] Standard errors were calculated from data on the variance of family means. No individual family data were available for 14-day post-irradiation survival

[b] Corresponding values for the selected and control populations from the selection experiment for 14-day post-irradiation survival were 42.4 and 1.9 respectively

Table 2. Linear regression coefficients for performance traits on generations of selection

Trait	Select population	Control populaton	Select–Control
Mating propensity	0.6 ±0.5	−3.1 ±0.5	3.9 ±0.6
% Survivors mating	0.5 ±0.5	−3.2 ±0.5	3.8 ±0.6
10-day post-irradiation survival	0.3 ±0.2	−1.5 ±0.3	1.9 ±0.3
7-day egg production	−1.6 ±0.4	−2.6 ±0.8	1.6 ±0.1
Egg-adult survival	0.3 ±0.5	0.7 ±0.6	−0.4 ±0.4
Level of inbreeding	2.88±0.12	2.65±0.12	0.22±0.21

It is apparent from Fig. 1 and Tables 1 and 2 that there was significant divergence for mating propensity between the Select and Control populations over the course of the experiment. Much of this divergence was the result of a decline in the Control population rather than an increase in the Select population. The decline in the Control population for nearly every measure of performance (Table 2) is likely the result of a deterioration of the environment over time, the effects of inbreeding, or both. We are inclined to put the most emphasis on the effects of inbreeding since most of the traits of interest are fitness related and are almost always highly subject to inbreeding depression. Complete pedigree data enabled us to determine the avarage level of inbreeding for both populations each generation. The level of inbreeding had reached more than 25% in both the Select and Control populations by generation 12. Since effective population size was maintained the same in the two populations throughout the course of the experiment, any divergence in means (but not the means themselves) would be independent of the inbreeding effect. It is obvious that whatever the cause for the decline in the Control, it was effectively countered by the selection process in the Select population. Since one of the goals in the selection was to develop a strain with increased mating propensity, the modest response was somewhat disappointing. In retrospect, the experiment would have been more definitive in sorting out inbreeding effects from environmental time trends if two controls and select populations could have been carried. Crossing of the controls would have pro-

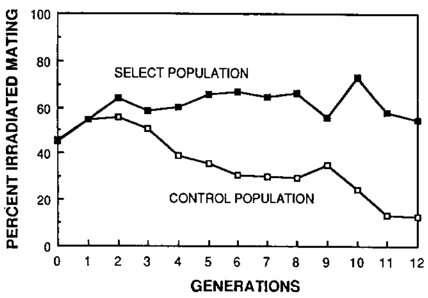

Fig. 1

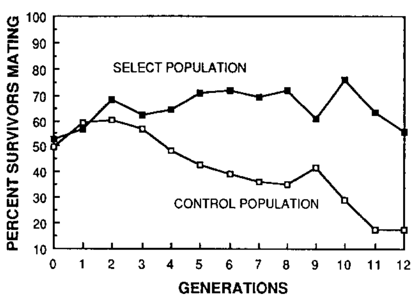

Fig. 2

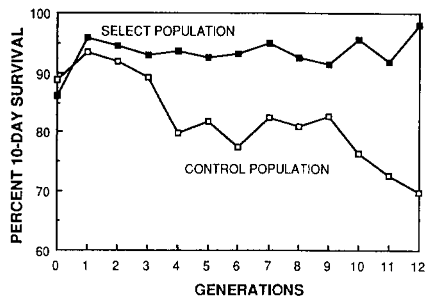

Fig. 3

Figs. 1–3. 1 Response to selection for mating propensity. 2 Correlated response of percent 10-day survivers mating when the selection criterion was percent irradiated mating. 3 Correlated response in 10-day post irradiation survival

vided clearer evidence on whether the decline was genetic, environmental, or both. Unfortunately, limitations on both space and funds precluded an experiment of such magnitude.

There is some evidence of a decline in environmental conditions, especially in the last two generations of the experiment where we experienced a precipitous drop in the mean performance of both the Select and Control populations for both mating propensity and percent survivors mating (Figs. 1 and 2). The Select population had reached a high of 73% for mating propensity in generation 10, which then dropped to 54.5% by generation 12. This had a significant impact on our measures of absolute response in the Select population using the linear regression method of estimation in Table 2. Evidence for poor environmental conditions in generation 12 are further substantiated by the mean performance of the Select and Control populations from our previous experiment where selection had been for radiation resistance. These populations were reared as contemporaries and treated the same as the new populations in generation 12 to get a comparative measure on 14-day post-irradiation survival for all populations we had developed in the total program. Means of these two populations in generation 12 were 42.4 and 1.9 (see footnote no. 2 in Table 1). This compares with means of 87.9 and 37.2 for these same populations in generation 20 of the earlier experiment (Enfield et al. 1983). These populations have both been maintained as large random breeding populations since completing the original experiment so the decline is not likely the result of inbreeding or drift. There is the possibility of some decline in the select population as a function of natural selection, but this is not likely a major factor since we saw no evidence of this effect when it was evaluated in the earlier experiment. Even if part of this difference was the result of natural selection in the population originally selected for radiation resistance, this would not account for the corresponding drop in the unselected population.

A comparison of the results in Figs. 1–3 support the hypothesis that most of the response to selection for mating propensity came from the difference in the fraction of survivors mating rather than major differences in survival per se, even though the latter was also significant when measured as the divergence between the two populations over time (Table 2). This argues that there are some genes affecting mating behavior that cannot be directly tied to survival. However, we cannot totally rule out that the survivors may simply be in a better state of overall vigor and that this plays a key role rather than genes whose primary effects are behaviorally related.

An estimate of realized heritability for the trait defined as 10-day post-irradiation mating propensity in males was obtained from the regression of accumulated response (as measured by the difference between the Select and Control population means) on accumulated selection differential. The estimate obtained in this way was 0.21 ± 0.04. It should be emphasized that this is a heritability of family means and that the trait measured is male mating propensity, even though selection is practiced for both sexes, since both males and females were saved from the families having the greatest male mating propensity.

Our results and interpretations are consistent with the pattern of results that have been observed for mating propensity studies in a number of other insect species. To our knowledge, this is the only selection experiment that has attempted to measure the effects of selection for mating behavior following high doses of irradiation. Kessler (1969) in a 24-generation selection experiment for mating speed in *Drosophila pseudooscura* found that nearly all response to selection was obtained in the first five generations of selection. Estimates of realized heritability for this period was approximately 13%. This experiment did not allow for separation of male and female contributions to mating speed. In an earlier experiment on *Drosophila melanogaster*, Fulker (1966) focused on performance of males only and determined that there was considerable dominance for fast mating speed. The narrow sense estimate of heritability of male mating speed in this experiment was 0.31. Spiess and Stankevych (1973) conducted a 16-generation experiment for mating speed in *Drosophila persimillis,* which resulted in a highly significant response. The total response in this case was a function of an effect on both sexes. Spiess (1970) provides an extensive review of much of the early work that was done in examining various aspects of the genetic basis for mating propensity in a number of *Drosophila* species.

Several studies support our interpretation that inbreeding can have a significant impact on mating propensity. Pendlebury and Kidwell (1974) measured the effects of rapid inbreeding on competitive mating ability, mating rate, and fecundity in *Drosophila melanogaster*. Drastic reductions in competitive ability and mating rate had occurred by an inbreeding level of $F=0.25$. Effects on sperm quality and quantity were less apparent. Roush (1986) observed severe inbreeding depression for mating behavior after one generation of brother-sister mating in the tobacco budworm. Ringo et al. (1986) found that drift lines derived from a highly heterozygous population of *Drosophila simulans* had a much reduced mating propensity in both sexes when compared with the base line from which they were derived. Similar effects of increased levels of homozygosity were observed for mating speed in *Drosophila melanogaster* by Connolly et al. (1974).

Continuation of the work reported here and earlier papers will center on a field testing program involving the cross of the two populations that have been selected for radiation resistance and mating propensity to evaluate the degree to which the selection response observed in the laboratory carries over to various measures of competitive ability in the field.

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