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**EFFECT OF SELECTING CEREAL LEAF BEETLE
(COLEOPTERA: CHRYSOMELIDAE) MALES BY AGE AND
FEEDING BEHAVIOR ON NONDIAPAUSE PROGENY**

S. G. Wellso and R. P. Hoxie¹

ABSTRACT

In a nondiapause culture of cereal leaf beetles, *Oulema melanopus* (Coleoptera: Chrysomelidae), females ovipositing within 20 days after emergence were considered nondiapause. However, sexually active males in the same generation could be nondiapause or prediapause. Changes in the nondiapause incidence were compared between progenies from > 15 day old males that were feeding actively and photopositive (considered 'nondiapause' males) and progenies from younger males (nonselected males). Nondiapause females increased by 19% (n = 35 generations) and decreased 22% (n = 31 generations) in the progenies of 'nondiapause' and nonselected males, respectively, suggesting that nondiapause males were selected in the former group, but prediapause males in the latter group substantially decreased nondiapause. In one generation, 14 progenies from individual pairs ranged from 21 to 100% nondiapause females, indicating that each sex in each parental pair was nondiapause, but nondiapause was incompletely expressed in most of the progenies.

The percentage of 'nondiapause' males was not significantly different than, and was strongly correlated to the percentage of nondiapause females of the same generation, indicating that nondiapause was not sex-linked, and that selecting males by age and behavior decreased the probability of dilution of nondiapause by prediapause males.

Cereal leaf beetles (CLB), *Oulema melanopus* (L.), are univoltine with an obligatory diapause (Hilterhaus 1965, Wellso 1974). In midwestern U.S., CLB emerge in late June through early July, and feed for about 3 weeks before dispersing to diapause sites for overwintering. In the spring, the beetles mate and oviposit. However, in Great Britain mating adults, eggs, and larvae have been observed in late summer prior to hibernation (diapause), suggesting the presence of a second generation (Hodson 1929).

Wellso and Hoxie (1981) reported that a nondiapause strain of CLB was selected and maintained at 26.7°C from females that initiated oviposition ca. 8 days after emergence. Although diapause CLB were present at greatly varying proportions in most generations, 4 of 29 nondiapause generations had 100% nondiapause females. However, diapause females were present in the progenies of these 4 generations, suggesting that in the parental generations, there was either an incomplete transfer of the nondiapause trait or prediapause males had mated successfully. Diapause of males, occurring ca. 13 days after emergence, was usually preceded by 2 days of decreased feeding in conjunction with a photonegative behavior. Prediapause males fed significantly more than nondiapause

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males during the first 8 days after emergence, indicating that nondiapause was genetically predetermined. Because prediapause or nondiapause males were incapable of fertilizing females earlier than 13 days after emergence, an asynchrony within a generation occasionally occurred between the periods of oviposition and sexual activity of males.

Studies of nondiapause adult insects usually focus on females because oviposition is easier to quantify as a nondiapause trait than mating behavior of males. This study was conducted to ascertain if age and behavior were reliable traits for selecting nondiapause males.

MATERIALS AND METHODS

Nondiapause cereal leaf beetles were derived from a nondiapause culture (Wellso and Hoxie 1981), and 66 generations were reared by a method similar to that used for diapause CLB (Hoxie and Wellso 1983). These generations were from the main culture (37 generations) and two cultures derived from the main culture (12 and 17 generations). CLB were maintained in growth chambers at $26.7 \pm 1^\circ\text{C}$, $70 \pm 10\%$ R.H. and L16:D8. Within each generation, each CLB was sexed upon emergence, and placed in a screen tube containing 2–3 barley seedlings. Daily feeding for up to 20 days was rated as: 0 (no feeding), 1 (few leaf punctures), 2 (light feeding), and 3 (heavy feeding). Beetles not feeding for two consecutive days (in diapause) or females (usually 0–1% of the active females) that did not oviposit during the feeding-monitoring period were removed from the nondiapause culture.

After oviposition was initiated, each female was transferred to a screened pot of barley for egg deposition, and males were subsequently placed in the oviposition cage. Each cage contained up to 20 females, and plants were changed every 3 days. One of two male selection methods for transferring males to the oviposition cage was assigned for each generation: (1) > 15 day old males that for 2 days prior to selection were not photonegative or feeding at a rating less than 2 (hereafter referred to as 'nondiapause' males) or (2) nonselected younger males. Although the assignment of the selection method to a generation was generally random, other conditions also influenced the assignment; e.g., if the CLB numbers were small and the parental nondiapause percentage was low, selecting for 'nondiapause' males was done to avoid losing the culture; emerged beetles in most generations were divided between this and other nondiapause studies (e.g., cross-breeding, L:D, field, or temperature) and the nonselected male method was commonly used; and, lastly, the three cultures were at times reared concurrently.

Within each of the two male selection groups, the numbers of each sex in the parent and progeny generations that were diapause or nondiapause during the trial period were recorded (those that died were excluded from the totals). The percentage of nondiapause beetles in each generation was derived from the ratio of individuals estimated to be nondiapause (ovipositing females or selected males) to individuals that survived the test period. This percentage was subtracted from that of the corresponding parent generation to show whether male selection changed the nondiapause percentages and in what direction. Means were compared between male selection groups by a Student's *t*-test. In the progenies of 18 selected and 14 nonselected male groups, the female nondiapause percentages and changes were compared to that of 'nondiapause' males of the same generation (Pearson correlations and paired *t*-tests). All statistical tests were performed using the Statistical Package for the Social Sciences (Nie et al. 1975).

To investigate the male's transfer of nondiapause, 24 of 102 males from one of the generations were randomly designated upon emergence to either (1) selected 18–21 day old males with the same 'nondiapause' behavioral criteria as previously defined ($n = 12$), or (2) 7–10 day old nonselected males ($n = 12$). Each male was paired with a nondiapause ovipositing virgin female from the same generation, and each pair was maintained in a screened tube containing barley plants. The percentage of cages with fertile eggs reflected the percentage of males (pre- or nondiapause) that successfully

Table 1.—Selection of cereal leaf beetle parental males by behavior: effect on nondiapause in their progeny.

| CLB types | Mean values per generation | | | | | | Selection method difference ^c |
|-------------------------|--------------------------------------|----------------------|--------|--------|----------------------|--------|--|
| | Parental male selection ^a | | | | | | |
| | Nondiapause | | | None | | | |
| | Parent | Progeny ^b | change | Parent | Progeny ^b | change | |
| Females | | | | | | | |
| Diapause (no.) | 12.1 | 6.9* | - 5.1 | 4.3 | 11.4** | + 7.1 | - 4.4 |
| Nondiapause (no.) | 13.6 | 16.2ns | + 2.6 | 13.2 | 11.4ns | - 1.8 | + 4.8 |
| Live (no.) ^d | 25.7 | 23.1ns | + 2.5 | 17.5 | 22.8ns | + 5.3 | - 0.3 |
| Nondiapause (%) | 57.3 | 76.6** | + 19.3 | 74.3 | 51.9** | - 22.4 | + 24.7** |
| Generations | | 35 | | | 31 | | |
| Males | | | | | | | |
| Diapause (no.) | 5.7 | 2.6ns | - 3.2 | 3.4 | 4.6ns | + 1.2 | - 2.0 |
| Nondiapause (no.) | 13.3 | 12.2ns | + 1.1 | 16.6 | 12.3ns | - 4.3 | - 0.1 |
| Live (no.) | 19.1 | 14.8ns | - 4.3 | 19.9 | 16.9ns | - 3.1 | - 2.1 |
| Nondiapause (%) | 75.1 | 84.3* | + 9.2 | 83.9 | 70.9** | - 13.0 | + 13.4* |
| Generations | | 18 | | | 14 | | |

*, $P < 0.05$; **, $P < 0.001$; ns, not significant ($P > 0.05$).

^a Males placed with nondiapause females: Nondiapause, males ≥ 15 days old and actively feeding 2 days prior to selection; None, males < 15 days old.

^b Significance of a difference between generations (Paired Student's t-test) within each parental male group.

^c Significance of a difference between parental male group progeny means (Student's t-test).

^d (Total emerged) - (total dead during the trial period).

mated and was compared to the nondiapause percentage of females of the same generation that emerged within 1–2 days of the selected males. The percentage of nondiapause females in each pair's progeny was recorded to indicate whether nondiapause was transferred from the parental male and whether the expression of nondiapause was 100%.

RESULTS AND DISCUSSION

The method of selecting parental males for placement with nondiapause females significantly affected the percentages of nondiapause females and the number of diapause females in their respective progenies (Table 1). In the 35 progenies of selected males, there was a 19.3% increase in nondiapause females which reflected the decrease of 5.1 diapause females per generation. In the 31 progenies of nonselected males, there was a 22.4% decrease in nondiapause females and an increase of 7.1 diapause females per generation, suggesting that both pre- and nondiapause parental males were involved in mating. These nondiapause changes were also observed in the progeny males, i.e., the percentage of 'nondiapause' males in the progeny of selected and nonselected males, increased 9.2% and decreased 13.0%, respectively.

There was no significant sexual difference between the number of diapause or nondiapause beetles, the percentage of nondiapause beetles, or the average nondiapause change (Table 2; paired t-tests, $P > 0.05$, $n = 32$ generations). However, for each variable, the correlation was significant (Pearson correlation, $P < 0.001$). This infers that,

Table 2.—Comparisons of cereal leaf beetle males to females within each of 32 generations^a.

| CLB status | Mean values per generation | | r-value ^b |
|-------------------------|-------------------------------|-----------------------------|----------------------|
| | Females $\bar{x} \pm S.E.$ | Males $\bar{x} \pm S.E.$ | |
| Diapause (no.) | 3.63 \pm 0.49 | 3.44 \pm 0.53 | 0.735 |
| Nondiapause (no.) | 13.69 \pm 1.75 | 12.25 \pm 1.27 | 0.738 |
| Live (no.) ^c | 17.31 \pm 2.08 | 15.69 \pm 1.62 | 0.695 |
| Nondiapause (%) | 77.81 \pm 2.86 | 78.42 \pm 2.72 | 0.938 |
| Nondiapause change (%) | -0.81 \pm 2.96 | -0.50 \pm 2.97 | 0.929 |

^a18 selected and 14 nonselected male progenies.

^bAll Pearson Correlation r-values significant ($P < 0.001$); no significant difference between female and male means (Paired Student's t-test, $P > 0.05$).

^c(Total emerged) - (total dead during the trial period).

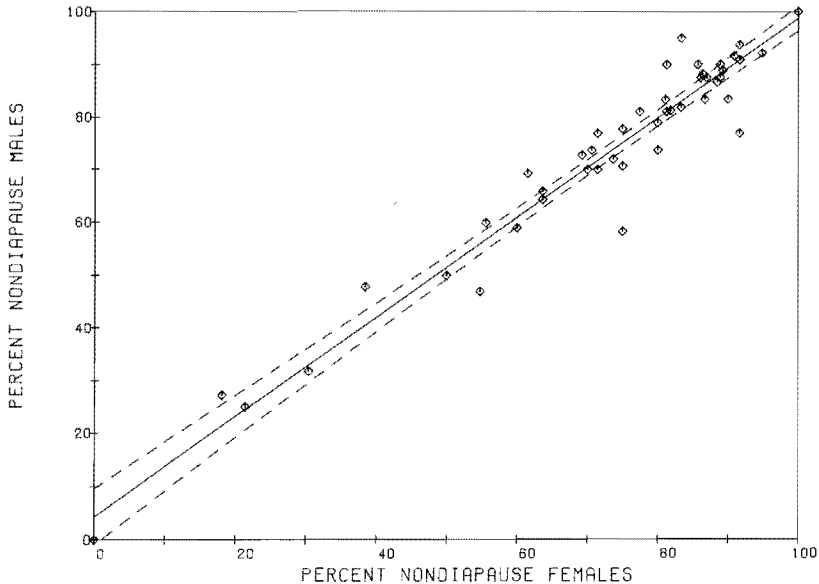


Figure 1. Relationship of cereal leaf beetle 'nondiapause' males to nondiapause females in the same generation ($Y = 4.18 + 0.95X$; $n = 45$, $r^2 = 0.95$, $P = 0.001$) with 95% CL.

if the nondiapause trait is transferred by the male and female on a 1:1 basis, the percentage of selected males in a generation would be a close estimation of the percentage of nondiapause males (Figure 1).

When males from one nondiapause generation were paired with nondiapause females, 100% (12 of 12) and 42% (5 of 12) of the males in the selected and nonselected males, respectively, inseminated the females (Table 3). The percentage of sexually active males in the nonselected group, approximated the percentage of nondiapause females (48%, 31

Table 3.—Percent of cereal leaf beetle females that are nondiapause in each progeny of selected pairs.

| Parent pair ^b (no.) | Selection of parental males for pairing with nondiapause females | | | | | | | | |
|-----------------------------------|--|--------------------------|-----|----------------------------|--------------------------|------------------------------|-----|-------|--|
| | nondiapause ^a (18–21 days old) | | | | | no selection (7–10 days old) | | | |
| | Fertile parents (no.) | Progeny females | | | Fertile parents (no.) | Progeny females | | | |
| live (no.) | | nondiapause (no.) (%) | | live ^c (no.) | | nondiapause (no.) (%) | | | |
| 1 | 1 | 14 | 7 | 50.0 | 0 | | | | |
| 2 | 1 | 16 | 7 | 43.8 | 0 | | | | |
| 3 | 1 | 7 | 5 | 71.4 | 0 | | | | |
| 4 | 1 | 30 | 18 | 60.0 | 0 | | | | |
| 5 | 1 | 0 | | | 1 | 15 | 8 | 53.3 | |
| 6 | 1 | 21 | 18 | 85.7 | 0 | | | | |
| 7 | 1 | 0 | | | 0 | | | | |
| 8 | 1 | 14 | 9 | 64.3 | 0 | | | | |
| 9 | 1 | 1 | 1 | 100.0 | 1 | 3 | 3 | 100.0 | |
| 10 | 1 | 10 | 4 | 40.0 | 1 | 0 | | | |
| 11 | 1 | 14 | 3 | 21.4 | 1 | 6 | 4 | 66.7 | |
| 12 | 1 | 3 | 1 | 33.3 | 1 | 7 | 5 | 71.4 | |
| Totals | 12 | 130 | 73 | | 5 | 31 | 20 | | |
| Progeny mean | | 13.0 | 7.3 | 57.0 | | 7.8 | 5.0 | 72.9 | |
| ± S.D. | | 8.5 | 6.2 | 24.2 | | 5.1 | 2.2 | 19.7 | |
| Parental source ^d | | 15 | 32 | 46.9 | | 16 | 32 | 50.0 | |

^aMales actively feeding and photopositive for 2 days prior to pairing.

^bMales were randomly assigned to each male group pair as they emerged.

^c(Total emerged) - (total dead during the trial period); zero values indicate eggs and larvae, but no adult emergence.

^dFemales from the same generation source as the selected pairs.

of 64 females) from the same generation. Of the 17 pairs with fertile eggs, 14 progenies survived to the adult stage. Ovipositing (nondiapause) females were present in every progeny, indicating that all parental males were nondiapause. However, the percentages of nondiapause females varied from 21 to 100% indicating that there was usually an incomplete transference of nondiapause.

To summarize, a 1:1 sexual transference of nondiapause is indicated by the nonsignificant differences between the percentage of nondiapause females and 'nondiapause' males in each generation. Although only nondiapause females were inseminated in each of the 66 generations, rejection of sexually competitive prediapause males usually occurred when male selection criteria were based on age and behavior. This was inferred from the increases and decreases in percentages of nondiapause females and 'nondiapause' males in the progenies of selected and nonselected males, respectively. However, generations with 100% nondiapause females rarely occurred and the percent nondiapause of the offspring usually decreased. This was also observed in the offspring of parental males that were known to have passed the nondiapause trait, indicating an incomplete transference of nondiapause to the progeny. Table 4 summarizes the types of CLB males encountered in a nondiapause culture. While nondiapause in the field has been observed infrequently, multiple generations would be advantageous to the CLB in the subtropics where host and environmental conditions are favorable most of the year.

Table 4.—Types of cereal leaf beetle males present within 20 days after emergence in a nondiapause culture and their effect on nondiapause in the next generation.

| Males present in a nondiapause culture | Diapause | | Sexual activity | Effect on nondiapause in the next generation |
|---|----------|------------------|--------------------|---|
| | status | age ^a | | |
| Diapause | early | 13 | none | none |
| Prediapause | late | >15 | active | decrease |
| Nondiapause | none | >15 | active | increase, usually incomplete |

^aDays after emergence.

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