BEET ARMYWORM (LEPIDOPTERA: NOCTUIDAE): EFFECTS OF AGE AT FIRST MATING ON REPRODUCTIVE POTENTIAL

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ABSTRACT

The effects of age at the first mating on the reproductive potential of the beet armyworm, *Spodoptera exigua* (Hübner), was studied in the laboratory. Both the fecundity and fertility of eggs laid were significantly affected ($P < 0.01$) by age of males and females at the time of mating. Delayed mating by females increased longevity but decreased fecundity and fertility ($P < 0.05$). Delayed mating by males increased longevity ($P < 0.05$) but decreased the number of spermatophores they transferred to females ($P < 0.01$). The number of spermatorphores transferred during mating affected female fecundity and fertility ($P < 0.01$). The optimum age for the first mating for both males and females was 1-2 days post-emergence. Delaying the first mating by either sex beyond 3-4 days post-emergence significantly, and adversely, impacted the reproductive potential of the beet armyworm.

Key Words: *Spodoptera exigua*, fecundity, fertility, longevity

RESUMEN

Fueron estudiados en el laboratorio los efectos de la edad en el momento del primer apareo sobre el potencial reproductivo del gusano de la remolacha, *Spodoptera exigua* (Hübner). La fecundidad y la fertilidad de los huevos puestos fueron significativamente afectadas ($P < 0.01$) por la edad de los machos y hembras en el momento del apareo. El retardo en el apareo en las hembras aumentó la longevidad pero disminuyó la fecundidad y la fertilidad ($P < 0.05$). El retardo en el apareo en los machos aumentó la longevidad ($P < 0.05$) pero disminuyó el número de espermatóforos transferidos a la hembra ($P < 0.01$). El número de espermatóforos transferidos a la hembra durante el apareo afectó la fecundidad y la fertilidad de las hembras ($P < 0.01$). La edad óptima para el primer apareo en machos y hembras fue 1-2 días después de la emergencia. El retado del primer apareo más allá de los 3-4 días de la emergencia redujo significativamente el potencial reproductivo del gusano de la remolacha en ambos sexos.

The beet armyworm, *Spodoptera exigua* (Hübner), was introduced into Oregon in 1876 and within a few years had migrated across the southern latitudes of the United States (Mitchell 1979). In recent years, the beet armyworm has become a serious economic pest of vegetables and cotton in the Southeast and mid-South (Douce & McPherson 1991, Layton 1994). The beet armyworm wreaked havoc on the cotton crop in the Lower Rio Grande Valley of Texas in 1995 (Summy et al. 1996). In the absence of heavy insecticide pressure on crops, populations of the beet armyworm often are maintained below economic levels by larval and pupal natural enemies (Ruberson et al. 1994). The beet armyworm has no effective natural enemies of its adult stage; however, it is a good factitious host for the ectoparasitic nematode, *Noctuidonema guyanense* Remillet and Silvain (Nematoda: Acugutturidae) in the laboratory (Rogers & Marti 1996). Before studying the effects of *N. guyanense* on the reproductive potential of *S. exigua*, we investigated the effects of age at mating on the reproductive potential of nematode-free moths.

MATERIALS AND METHODS

Experimental insects were from an established colony of the beet armyworm maintained on a pinto bean-based diet at the ARS Insect Biology and Population Management Research Laboratory, Tifton, GA (Burton 1967). As moths emerged, they were placed individually in a 0.6-liter cardboard container, provided 10% honey solution for nourishment, and maintained at 27°C and 80% RH in a 14:10 h (L:D) photoperiod. To determine the effect of age at first mating on fecundity and fertility in the beet armyworm, pairs of different male/female age combinations were established. Tests encompassed 19 trials, each of which contained 19-24 replicated pairs ranging in age from 1 to 9 days post-emergence. Mating pairs were maintained as mentioned above in 0.6-liter cardboard cages with the top and bottom covered with netting and paper towel lids. Cages were lined with waxed paper to facilitate removal and counting of eggs. Cages were examined daily to record data on moth mortality/longevity and to collect eggs. Eggs were incubated 4 days at 30°C. The number of unhatched eggs and viable larvae was used to compute daily fecundity and fertility for each pair. Moths were maintained in their respective cages until both died. Dead females were dissected to determine the number of harbored spermatophores.

All data were subjected to an analysis of variance by the General Linear Model Procedure, and significantly different means were separated by the least significant difference (LSD) test (SAS Institute 1989). Pearson correlation coefficients also were computed to document significant interactions among biological parameters.

RESULTS AND DISCUSSION

Among the 443 pairs, 112 females received no spermatophores, 145 females received a single spermatophore, and one female each received as many as 7, 8, or 9 spermatophores (Table 1). An average of 1.55 spermatophores was transferred to females among all matings. Discounting the 112 pairs with which no spermatophores were transferred, the remaining 331 pairs transferred an average of 2.07 spermatophores. The number of spermatophores transferred during mating was significantly affected by male age (r = -0.69; $P < 0.01$; F = 7.70; d.f. = 8,424), female age (r = -0.56; $P < 0.05$; F = 6.45; d.f. = 8,424), and combined pair ages (r = -0.76; $P < 0.01$; F = 7.87; d.f. = 10,422) at the first mating. Also, the number of spermatophores transferred during mating significantly affected the number of eggs laid (r = 0.73; $P < 0.01$; F = 1.68; d.f. = 9,423), the percentage of eggs hatching (r = 0.81; $P < 0.01$; F = 24.66; d.f. = 9,423), and the number of resulting viable larvae (r = 0.84; $P < 0.01$; F = 23.26; d.f. = 9,423). The lone female receiving 7 spermatophores laid 1,993 eggs and the 6 females receiving 6 spermatophores laid an average of 1,464.8 eggs, of which 99.4 and 66.4% hatched, respectively (Table 1). One female received 9 spermatophores. However, these were small and shriveled, and none of her eggs hatched. Females receiving only 1 or 2 spermatophores laid an average 500.1 to 831.2 eggs, of which 16.3 to 50.9% hatched. Females receiving no spermatophores laid an average of only 263.9 eggs, none of which hatched. Thus, with the beet armyworm, it appears that multiple spermatophores must be received by females for maximum reproductive capacity to be realized. The number of spermatophores transferred during mating seemed to have no effect on the longevity of females (r = -0.37, $P > 0.05$) or males (r =-0.22, $P > 0.05$). A correlation between spermatophore transfer at mating and female fecundity and fertility also has been reported for *Trichoplusia ni* (Hübner) (Noctuidae) (Ward & Landolt 1995), *S. frugiperda* (J. E. Smith) (Rogers & Marti 1994), and *Atteva punctella* (Cramer) (Yponomeutidae) (Taylor 1967). It appears that unsuccessful matings (evidenced by transfer of viable sperm) and low fertility among lepidopteran species are not uncommon, especially if the initial mating after emergence is delayed by 3 or more days (Unnithan & Paye 1991, Proshold 1996, Ellis & Steele 1982, Proshold et al. 1982, Lingren et al. 1988).

The age of females at their first mating significantly affected fecundity (r = -0.69; $P < 0.01$; F = 5.84; d.f. = 8,435), fertility (r = -0.69; $P < 0.01$; F = 15.45; d. f. = 8,435), longevity (r = 0.74; $P <= 0.01$; F = 8.21; d.f. = 8,431), and the number of viable larvae (r = -0.72; $P < 0.01$; F = 14.88; d.f. = 8,435). Females mating on the first or second day post-emergence received significantly more spermatophores ($P < 0.01$; F = 6.45; d.f. = 8,432) than females mating at an older age (Table 2). Percentage hatch of eggs laid by females mating during their first 3 days was significantly higher than for eggs laid by older females. Although mating by females at an early age enhances their fecundity and fertility, it also significantly shortens their life span (Table 2). Females mating by day 3 post-emergence lived an average 12.4 to 17.4 days, while those mating at an

TABLE 1. EFFECTS OF SPERMATOPHORE TRANSFER ON REPRODUCTIVE POTENTIAL OF THE BEET ARMYWORM

No. Spermatophores Transferred	N	No. Eggs Laid ($\bar{x} \pm$ S.E.)[1]	% Eggs Hatching ($\bar{x} \pm$ S.E.)[1]	Longevity (Days)	
				Female ($\bar{x} \pm$ S.E.)[1]	Male ($\bar{x} \pm$ S.E.)[1]
0	112	263.9 ± 36.6 d	0 ± 2.8 d	22.3 ± 0.7 a	17.1 ± 0.7 a
1	145	500.1 ± 32.2 a	16.3 ± 2.4 cd	19.3 ± 0.6 a	14.1 ± 0.6 a
2	82	831.2 ± 42.8 c	50.9 ± 3.2 b	16.9 ± 0.8 a	12.6 ± 0.8 a
3	44	653.2 ± 58.4 c	44.1 ± 4.4 bc	18.5 ± 1.1 a	14.6 ± 1.1 a
4	21	902.3 ± 84.5 c	44.7 ± 6.4 b	16.0 ± 1.6 a	12.1 ± 1.5 a
5	20	937.6 ± 86.6 bc	49.6 ± 6.6 b	16.9 ± 2.9 ab	13.7 ± 1.6 a
6	6	1464.8 ± 158.0 ab	66.4 ± 11.9 ab	12.7 ± 2.9 ab	11.0 ± 2.8 a
7	1	1993.0 ± 387.1 a	99.4 ± 29.3 a	19.0 ± 7.3 a	18.0 ± 6.9 a
8	1	801.0 ± 387.1 c	78.7 ± 29.3 a	9.0 ± 7.3 a	8.0 ± 6.9 a
9	1	681.0 ± 387.1 c	0. ± 29.3 d	14.0 ± 7.3 a	13.0 ± 6.9 a

[1]Means within a column followed by different letters are significantly different, $P < 0.05$ by the SAS LSD test.

TABLE 2. EFFECTS OF FEMALE AGE AT FIRST MATING ON THE REPRODUCTIVE POTENTIAL OF THE BEET ARMYWORM.

Female Age (Days)	N	No. Spermatophores Received ($\bar{x}$ ± S.E.)[1]	No. Eggs Laid ($\bar{x}$ ± S.E.)[1]	% Eggs Hatching ($\bar{x}$ ± S.E.)[1]	Female Longevity[2] ($\bar{x}$ ± S.E.)[1]
1	91	2.4 ± 0.2 a	885.8 ± 44.2 a	44.5 ± 3.3 a	16.6 ± 0.7 c
2	24	1.8 ± 0.3 a	730.0 ± 86.1 a	46.8 ± 6.5 a	12.4 ± 1.4 d
3	72	1.6 ± 0.2 b	549.4 ± 49.7 b	41.5 ± 3.8 a	17.4 ± 0.8 bc
4	24	0.9 ± 0.3 c	466.8 ± 86.1 c	9.8 ± 6.5 c	20.3 ± 1.4 a
5	70	1.8 ± 0.2 ab	533.7 ± 50.4 bc	24.9 ± 3.8 b	19.9 ± 0.8 ab
6	24	0.7 ± 0.3 c	720.1 ± 86.1 ab	5.3 ± 6.5 c	21.2 ± 1.5 a
7	45	1.3 ± 0.2 bc	381.2 ± 86.1 cd	10.4 ± 4.7 c	20.0 ± 1.1 a
8	24	1.5 ± 0.3 b	504.8 ± 86.1 c	11.6 ± 4.5 bc	22.8 ± 1.4 a
9	70	1.0 ± 0.2 c	318.8 ± 50.4 d	3.9 ± 3.8 c	22.7 ± 0.9 a

[1]Means within a column followed by different letters are significantly different, $P < 0.05$ by the SAS LSD test.
[2]Days

older age lived for 20 days or more. The number of eggs laid by females also significantly affected their longevity (r = -0.51; P < = 0.05; F = 1.36; d.f. = 37,402). Also, egg fertility was inversely correlated with female longevity (r = -0.67; $P < 0.05$; F = 5.32; d.f. = 37,402). Females laying an average of 676.8 or more eggs had an average longevity of up to 12 days, whereas females laying an average of fewer than about 400 eggs lived an average of more than 15 days. The fertility of eggs laid by females living fewer than 12 days averaged 56.4 to 93.7%, whereas the fertility of eggs from females living more than 15 days averaged less than 27%. These relationships among reproductive parameters of females are not unique to *S. exigua*. These same relationships exist in other lepidopteran species, e.g., *Spodoptera littoralis* (Boisduval) (Ellis & Steele 1982), *Lymantria dispar* (L.) (Lymantridae) (Proshold 1996), *Chilo partellus* (Swinhoe) (Pyralidae) (Unnithan & Paye 1991), *Heliothis virescens* (F.) (Noctuidae) (Proshold et al. 1982), *Pectinophora gossypiella* (Saunders) (Lingren et al. 1988), and *S. frugiperda* (Rogers & Marti 1994).

The age of males at first mating significantly affected the number of spermatophores transferred (r = -0.69; $P < 0.01$; F = 7.70; d.f. = 8.424), the number of eggs laid by their mates (r = -0.59; $P < 0.01$; F = 14.09; d.f. = 8,435), fertility of mate's eggs (r = -0.65; $P < 0.01$; F = 14.09; d.f. = 8,435), the number of resulting viable larvae (r = 0.61; $P < 0.01$; F = 9.94; d.f. = 8,435), and the longevity of males after their first mating (r = -0.65; $P < 0.01$; F = 8.77; d.f. = 8,425 (Table 3). Males mating on days 1-4 post-emergence transferred significantly more spermatophores ($\bar{x}$ = 1.82-2.23) than males mating on days 6-9 ($\bar{x}$ = 0.7-1.2). Significantly more eggs were laid by females mating with 1- to 3-day old males ($\bar{x}$ = 701.1-787.4) than females mating with 7- to 9-day old males ($\bar{x}$ = 343.6-371.6). The percentage of eggs hatching from eggs of females mating with 1- to 3-day old males averaged about 45%, compared with 5.2-19.9% hatching of eggs from females mating with 4- to 9-day old males. Although the total longevity of males was only weakly correlated with mating age (r = 0.30; $P > 0.05$; F = 3.54; d.f. = 8,425), their longevity after mating averaged 15.8 to 17.6 days for those mating on day 1-3 post-emergence, but only 10.6 to 14.5 days for those mating 4-9 days post-emergence. Female longevity was only weakly correlated (r = 0.35; $P > 0.05$; F = 5.72; d.f. = 8,431) with male age at mating.

Although the reproductive status of males affected the reproductive potential of the beet armyworm, their contributions had less impact than those of females. For the fall armyworm, the age of males at first mating had little impact on the reproductive potential of female mates (Rogers & Marti 1994). However, in *H. virescens* and *L. dispar*, the age of males at first mating affected spermatophore and/or sperm transfer to females during mating (Proshold 1996, Proshold & Bernon 1994). In *A. punctella,* the failure of female fertility is usually due to the failure of males to transfer sperm during mating, but there was no relationship between potency of sperm and age of males at mating (Taylor 1967). In *C. partellus*, the age of males had no effect on mating activity up to 5 days post-emergence, nor did it affect the fecundity or fertility of female mates (Unnithan & Paye 1991).

Just as the age of females and males at mating independently affected the reproductive potential of the beet armyworm, the combined age of mating pairs interacted to significantly affect the number of spermatophores transferred (r = -0.76; $P < 0.01$; F = 7.87; d.f. = 10,422), the number of eggs laid (r = -0.78; $P < 0.01$; F = 12.45; d.f. = 10,433), fertility of eggs (r = -0.82; $P < 0.01$; F = 22.34; d.f. = 10,433), the number of resulting viable larvae (r = 0.81; $P < 0.01$; F = 19.36; d.f. = 10,433), and the longevity of female partners (r = 0.67; $P < 0.01$; F = 5.83; d.f. = 10,429). Mating moths with a combined age of 2 days transferred significantly more spermatophores ($\bar{x}$ = 3.3) than pairs with a combined age of 4 days or more ($\bar{x}$ = 0.7-2.1). Pairs with a combined age of 2 or

TABLE 3. EFFECTS OF MALE AGE AT FIRST MATING ON THE REPRODUCTIVE POTENTIAL OF THE BEET ARMYWORM.

					Longevity (Days)	
Male Age (Days)	N	No. Spermatophores Transferred ($\bar{x} \pm$ S.E.)[1]	No. Eggs Laid by Female[2] ($\bar{x} \pm$ S.E.)[1]	% Eggs Hatching ($\bar{x} \pm$ S.E.)[1]	Male Longevity ($\bar{x} \pm$ S.E.)[1]	Female Longevity[2] ($\bar{x} \pm$ S.E.)[1]
1	72	2.2 ± 0.2 a	787.4 ± 51.5 a	44.7 ± 3.8 a	18.6 ± 0.7 b	18.0 ± 0.9 b
2	24	1.8 ± 0.3 a	730.0 ± 89.2 a	46.8 ± 6.6 a	14.7 ± 1.2 c	12.4 ± 1.5 c
3	71	2.2 ± 0.2 a	701.1 ± 51.5 ab	44.9 ± 3.8 a	18.8 ± 0.7 ab	17.4 ± 0.9 b
4	23	1.8 ± 0.3 a	489.8 ± 91.2 c	19.9 ± 6.7 b	18.5 ± 1.2 b	23.7 ± 1.5 a
5	93	1.6 ± 0.2 ab	535.9 ± 45.3 bc	20.4 ± 3.3 b	19.9 ± 0.6 a	20.6 ± 0.8 ab
6	24	0.7 ± 0.3 c	720.1 ± 89.2 a	5.3 ± 6.6 c	20.6 ± 1.3 a	21.2 ± 1.6 a
7	46	0.9 ± 0.2 c	371.6 ± 64.5 c	5.2 ± 4.7 c	17.6 ± 0.8 b	18.4 ± 1.1 b
8	43	0.9 ± 0.2 c	437.4 ± 66.7 c	7.0 ± 4.9 bc	19.2 ± 0.9 a	19.5 ± 1.1 b
9	47	1.2 ± 0.2 bc	343.6 ± 63.8 c	14.6 ± 4.7 bc	21.3 ± 0.8 a	21.2 ± 1.1 a

[1]Means within a column followed by different letters are significantly different, $P < 0.05$ by the SAS LSD test.
[2]Females mated with males of respective age.

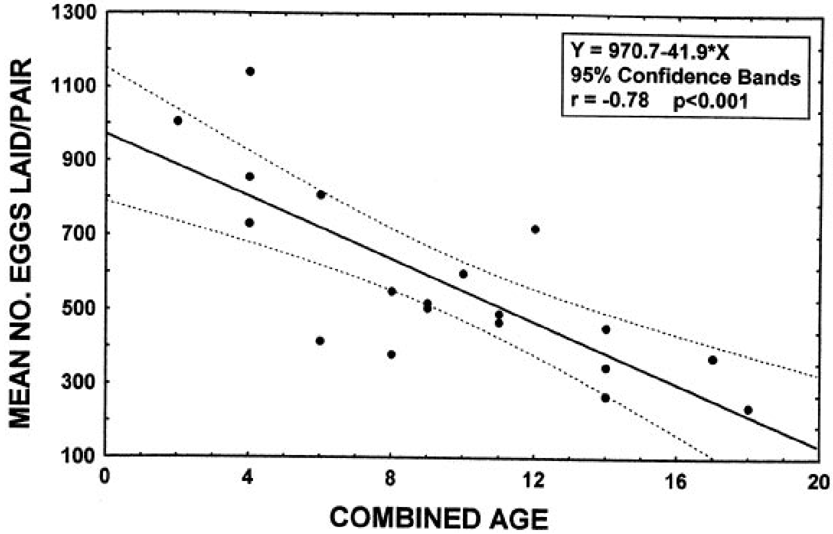

Fig. 1. Fecundity of the beet armyworm as a function of combined age of mating pairs on their first mating.

4 days at mating produced significantly more eggs (x? = 907.4) than pairs with a combined age greater than 6 days ($\bar{x}$ = 238.7-610.9) (Fig. 1). Eggs laid by females from pairs with a combined age of 2 or 4 days at first mating produced eggs having a significantly higher percentage hatching ($\bar{x}$ = 57.7-61.1%) than eggs from older pairs ($\bar{x}$ = 1.8-44.4%). If either mate of the pair were aged, the contributions of its younger mate were greatly minimized (Fig. 2). The number of viable larvae produced was significantly greater in mating pairs with a combined age of 2-4 days ($\bar{x}$ = 637.1-767.7) than the number produced by pairs with a combined age greater than 6 days ($\bar{x}$ = 9.8-316.7). Females from pairs having a combined age of 2-6 days at first mating lived significantly fewer days ($\bar{x}$ = 15.1-16.2) than females of pairs having a combined age greater than 8 days ($\bar{x}$ = 19.6-21.9).

In summary, the reproductive potential of the beet armyworm is significantly impacted by the age of both males and females at their first mating. However, there is a trade-off between enhanced reproductive potential of young moths and longevity of ovipositing females, i.e., more fecund/fertile moths have a shorter life span than females with a reduced reproductive potential. One to 2 days post-emergence is the optimum age for the first mating for both sexes for maximum reproductive potential. Hence, to evaluate the effects of adult mortality factors, e.g., parasitic nematodes, on the reproductive potential of the beet armyworm, it will be necessary to standardize the age of young moths.

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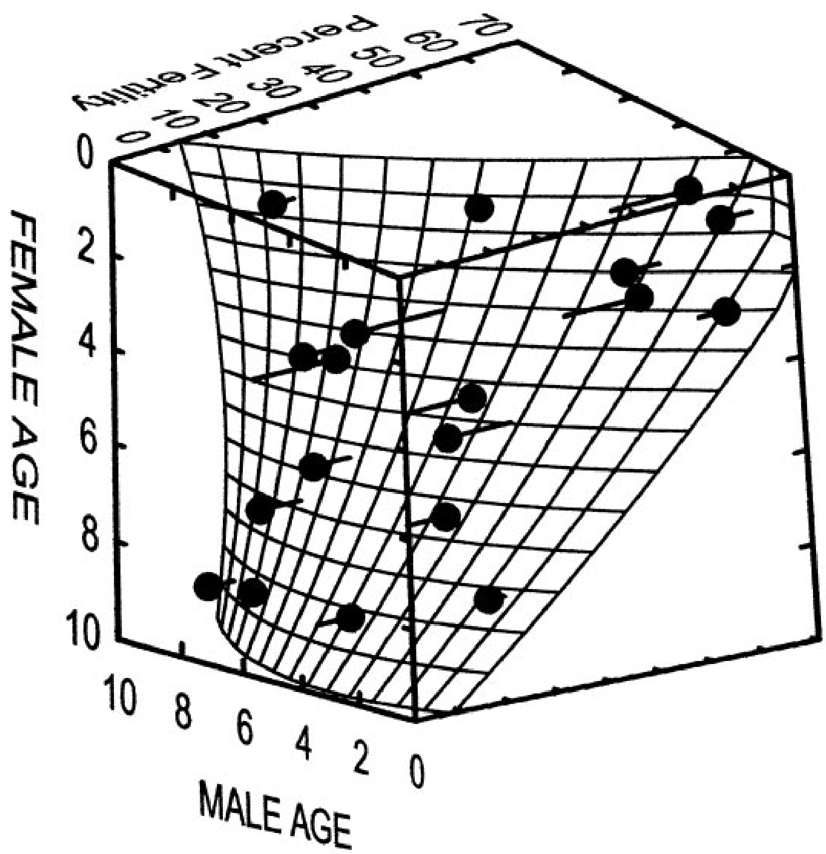

Fig. 2. Fertility of beet armyworm eggs as a function of male and female age at the first mating of a pair.

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