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Research

Stored-Product

Effect of Delayed Mating on Longevity and Reproductive Performance of *Lasioderma serricorne* (Coleoptera: Anobiidae)

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Abstract

In recent times, research has focused on integrated pest management approaches using nonchemical alternatives such as mating disruption for the control of stored product insect pests. In this study, we examined the effect of imposed delayed mating on the longevity and reproductive performance of the cigarette beetle, *Lasioderma serricorne* (F.), a serious insect pest of value added grain-based products, tobacco products, and spices. Delayed mating, progressing 0–14 d, was imposed on both sexes simultaneously, on males only, and on females only. Insects were observed daily for longevity, and F_1 progeny was recorded 7–10 wk after mating pairs were placed together. Unmated adults lived significantly longer than mated adults, and mated females lived significantly longer than mated males. However, the length of the period of mating delay did not significantly affect the longevity of mated adults. Progeny production decreased with the age of adults at mating. The number of progeny produced when mating delay was imposed on both sexes simultaneously or on females only was significantly lower than when mating delay was imposed on males only. Hence, females were more adversely affected by delayed mating than males. Findings from this study may provide information for the development of mating disruption techniques that can delay mating and may be effective in keeping populations of *L. serricorne* below levels that would warrant a control action.

Key words: cigarette beetle, mating disruption, mating delay, methyl bromide alternative, stored product

Mating disruption techniques usually involve the use of synthetic sex pheromones that mimic the naturally produced female sex pheromone. Mating disruption is a method in which an unnaturally high level, many milligrams a day, of synthetic pheromone is released into a treated area. Males are unable to locate females that are releasing pheromone at normal levels of nanograms to micrograms per day. Males are considered either physiologically 'confused', in that their nervous system cannot properly interpret the extremely high levels of pheromone and thus, do not respond to females, or they engage in 'false trail following', such that they spend a majority of time orienting to synthetic pheromone dispensers and never find females (Cardé and Minks 1995, Phillips et al. 2000). The important result is that many females go unmated during the mating disruption event, thus reducing egg laying and ultimately the overall population is reduced or goes extinct (Welter et al. 2005, Fitzpatrick 2006, Mahroof and Phillips 2014). Pheromone mating disruption programs are highly selective, with only the primary target species responding to the pheromone. Kovanci et al. (2005) compared mating disruption with using organophosphate insecticides for the management of oriental fruit moth, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae) in apple orchards and found that mating disruption could be an effective alternative to organophosphate treatments. Mating disruption has been successfully employed in commercial tree nuts and orchards against many insect pests; e.g., the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) in walnuts, apples, and pears (Angeli et al. 1999, Calkins and Faust 2003, Stelinski et al. 2013, İşci et al. 2016).

Limited studies on mating disruption have been carried out on stored product insect pests. These studies have been focused on Lepidopteran pests such as the Indian meal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) (Mbata 1985, Fadamiro and Baker 2002), the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) (Fadamiro and Baker 2002) and the Mediterranean flour moth, *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) (Athanassiou et al. 2016). Fadamiro and Baker (2002) demonstrated the potential of pheromone-based mating disruption as a management strategy for *P. interpunctella* and *S. cerealella*. The authors reported a significant reduction in the proportions of mated females of both species. Athanassiou et al. (2016) evaluated the application of mating disruption using pheromone-baited sticky traps and oviposition traps in storage facility of amylaceous products and found that oviposition and subsequent larval development was reduced in the treated facility.

No mating occurs if mating disruption programs are completely effective, but programs can still be useful in reducing population growth if finding mates is more difficult resulting in a delay in the time of mating. Delayed mating, regardless of the mechanism causing the delay, can have negative impacts on reproduction (Ellis and Steele 1982, Lingren et al. 1988, Angeli et al. 1999, Fadamiro and Baker 1999, Athanassiou et al. 2016). Mbata (1985) reported that a delay in mating in females resulted in a significant reduction in the number of eggs laid by *P. interpunctella* with mature eggs retained in the ovaries of the female. According to Huang and Subramanyam (2003), fecundity in female *P. interpunctella* significantly decreased by about 25 eggs for each day mating was delayed. Huang and Subramanyam (2003) also reported that delaying mating in both sexes for 5 d resulted in the production of nonviable eggs by the female. Gerken and Campbell (2018) showed that mating delay for the stored product pest beetles *Trogoderma variabile* Ballion (Coleoptera: Dermestidae) and *T. inclusum* LeConte resulted in reduced number of eggs laid, but only after 10 and 15 d, respectively. This was longer than reported for *P. interpunctella*, and even out to greater than 15 d delay, there was still some progeny production. In addition to fecundity being affected by delays in mating, delaying mating increased adult longevity over insects that mated soon after emergence and unmated adults usually lived longer than mated adults (Singh and Wilbur 1966, Ellis and Steele 1982, Lingren et al. 1988, Yu 2008, Gerken and Campbell, 2018).

The cigarette beetle, *Lasioderma serricorne* (F.), is a major insect pest of grain-based products, spices, cocoa, dried medicinal products, tobacco, tobacco-based products, and other durable commodities (Howe 1957, Arbogast 1991, Ashworth 1993, Dimetry et al. 2004, Mahroof and Phillips 2008). The larva causes most of the damage due to feeding (Minor 1979), but adults can also damage packaged commodities by chewing entry and exit holes (Howe 1957, USDA 1972). Adults are short-lived, do not feed, and mate within a few days after emergence (Howe 1957, Coffelt and Burkholder 1973, Minor 1979). The female produces the sex pheromone serricornin, with amounts produced peaking 4–5 d after emergence. Therefore, females may not be receptive to male copulatory attempts before 2–3 d of age (Coffelt and Burkholder 1972).

There has been a growing need for alternative, nonchemical control options for *L. serricorne* (Adler 2003, Roesli et al. 2003, Conyers and Collins 2006, Mahroof and Phillips 2007, Yu 2008, Mahroof and Phillips 2014). This has particularly become important following the ban of methyl bromide (EPA 2006) and the development of resistance to phosphine (e.g., Savvidou et al. 2003, Sağlam et al. 2015, Fukazawa and Takahashi 2017). Mahroof and Phillips (2014) studied the effect of mating disruption on *L. serricorne* using the synthetic form of serricornin. A reduction in mating success and subsequently a significant decline, about 36–55%, in the population size of succeeding generation was reported.

Like many Lepidopteran pests, *L. serricorne* adults are short-lived and mate within a few days after emergence. The sooner a delay in mating can induce negative effects on fecundity, the more likely mating disruption tactics are going to be effective in managing pest populations. Therefore, the objective of this study was to investigate the effect of mating delay on *L. serricorne* fecundity and longevity.

Materials and Methods

Test Insects

Insects used for this study were from colonies which had been maintained at the Stored Products Entomology Research Laboratory at South Carolina State University, Orangeburg, SC since 2010. Colonies were established by transferring newly emerged adults to 950 ml rearing jars (Ball Corporation, Broomfield, CO) containing a 95:5 ratio of whole wheat flour and brewer's yeast. After 48 h of egg laying, the adults were removed, and the rearing jars were kept in an incubator (I-36VL; Percival Scientific Inc., Perry, IA) for 31–35 d at 26.2 ± 0.1°C and 50.2 ± 0.5% RH to attain the pupal stage of the insect. The pupae were sexed using differences in the genital papillae, which are three-segmented and divergent in the females but globular and not projecting in males (Halstead 1963). The pupae after sexing were kept separately in jars containing a small amount of the rearing diet to provide a suitable substrate for the insects. Adults that emerged in each jar were collected promptly and kept in separate jars to be used when required. To distinguish female from male beetles when put together, the elytra of the female were marked with a small dot of correction fluid. Adults of between 0 and 14 d old were used in this study.

Effect of Delayed Mating on Adult Longevity

The longevity of the mated insects was determined by pairing one male and one female of the same age (0–14 d old) in a 5 cm high, 2 cm diameter plastic vial that contained 2 g of the diet. There were 20 mated-pairs for each age. Additionally, 0-d-old males and females were paired and held for 48 h before separating ($n = 20$), and the longevity was evaluated. This treatment was to determine if frequency of mating or other male–female interactions could affect the longevity of the insects. Twenty unmated male adults and 20 unmated female adults were placed individually in vials with 2 g of diet to serve as controls. All vials were checked daily up to approximately 7 wk to record the longevity of each adult.

Effect of Delayed Mating on Progeny Production

Delayed mating (0–14-d delay) was applied on both sexes of the beetle simultaneously, females only, and males only. To establish delayed mating on both sexes simultaneously (referred to as same age), one virgin male beetle aged 0–14 d was paired with a virgin female beetle of the same age in a 5 cm high, 2 cm diameter plastic vial that contained 2 g of the diet. In another experiment, female beetles only were subjected to delay mating (referred as female-varied) where one 0-d-old virgin male was paired up with a 0–14-d-old virgin female in a 10 cm high, 2 cm diameter plastic vial that contained 5 g of the diet. Finally, a third delayed mating experiment as described above was repeated. This time, a 0-d-old virgin female was paired with a 0–14-d-old virgin male (referred to as male-varied) in a 10 cm high, 2 cm diameter plastic vial that contained 5 g of the diet. Each mating treatment was replicated ten times.

All experimental vials were kept in an incubator at approximately 27.6 ± 0.1°C and 60.8 ± 0.8% RH and the adults were kept in the vials throughout the duration of the experiment. The number of F_1 adults that developed in each vial was recorded weekly for 4 wk beginning 7 wk after setting up until 10 wk.

Data Analyses

Lifespan models

Data for all lifespan were analyzed using PROC GLM, SAS software v. 9.4 (SAS Institute, Cary, NC) for the interaction between age at mating and sex of the beetle. In these analyses, longevity, i.e., the total number of days that the beetles lived for, was considered as the dependent variable while age at mating and sex of the beetles were main effects in the model. Replicate was used in the model as a random effect. If the main effect was significant in the model, then LS-means were Tukey-adjusted. Models for each sex were also run to analyze age-specific differences between controls and each day of mating delay for each of the sexes. In these models, longevity was used as the dependent variable while replicate was used as a random effect.

Progeny models

To assess differences in the progeny production across days of mating delay, we used a generalized linear mixed model using PROC GLIMMIX (SAS software) with total number of progeny produced as the dependent variable. Experiment (male-age-varied, female-age-varied, or same aged) was the main effect as well as the age of males and females nested within experiment. Replicates were used as random effects. Tukey-adjusted LS-means were calculated for significant effects.

Net reproductive rate calculation

Daily progeny emergence was estimated by dividing the total progeny emerged in a week by 7, which assumes an equal proportion of progeny emergence on each day of the week. To calculate net reproductive rate, R_o, we used survivorship (l_x) for each age class or day, including those where beetles were not mated. Survivorship is defined as the proportion of the original females alive on a given day (age class). Mortality (d_x) is the proportion of females that have died at a given age class and daily mortality rate ($q_x = d_x/l_x$) is the number that have died over time. Daily progeny emergence counts were used to calculate the mean reproductive rate per day (m_x), which is the number of offspring divided by the number of females at a given age class. Finally, the net reproductive rate was calculated ($R_o = \Sigma l_x m_x$), which is the average number of daughters a female produces and accounts for age-specific mortality and progeny emergence of the cohort. A jack-knife procedure was used to determine the 95% CI for R_o values by dropping individual replicates and recalculating R_o.

Results

Effect of Delayed Mating on Adult Longevity

Age ($F_{16} = 29.71$, $P < 0.0001$) and sex ($F_1 = 10.81$, $P = 0.0011$) were significantly different when analyzed for differences in adult longevity but there was no significant interaction between age at mating and sex ($F_{16} = 1.27$, $P = 0.2080$). Overall, males had a shorter lifespan (18.1 d) than females (19.0 d). Unmated beetles had significantly greater longevity (29.6 d) than beetles that were mated at any of the different points in time, but there was no consistent trend in longevity in relation to days of delay in mating (Table 1).

When longevity is evaluated separately for each sex, females age at first mating (0–14 d) led to significantly different longevity ($F_{16} = 15.14$, $P < 0.0001$). However, as in the full interaction model, there were no consistent patterns of increased longevity as days of mating delay increased (Fig. 1), but virgin females had significantly longer lifespans (31.2 d) than mated females at any amount of delay (Table 2). For males, longevity was also significantly different among age at first mating ($F_{16} = 15.76$, $P < 0.0001$). However, as with females, there was no specific pattern of longevity change with increasing time of mating delay, except that unmated control males lived significantly longer (27.9 d) than individuals that mated (Fig. 1, Table 2). No mated adult survived longer than 37 d, but with unmated males and females, we recorded longevity up to 42 and 50 d, respectively. There was a trend for increased and less variable longevity when pairs were held together for 48 h and then separated (Fig. 2).

Table 1. Mean longevity (in days) of unmated *Lasioderma serricorne* adults and mated adults delayed from mating for the same amount of time (0–14 d)

Age of adults at mating	Mean longevity (days)	Tukey Grouping
Control, unmated	29.6	A
0, separated after 48 h	21.1	B
0, kept together	19.2	BCD
1	15.3	F
2	16.5	DEF
3	17.1	CDEF
4	18.1	CDEF
5	17.8	CDEF
6	18.5	BCDE
7	18.6	BCDE
8	18.0	CDEF
9	16.7	DEF
10	15.9	EF
11	17.3	CDEF
12	17.5	CDEF
13	18.7	BCDE
14	19.8	BC

Means followed by different letters are significantly different (Tukey's honest significant difference test, $P < 0.05$). $n = 40$.

Effect of Delayed Mating on Progeny Production

For progeny production, the female-varied, male-varied, and same-age treatments were significantly different ($F_2 = 23.60$, $P < 0.0001$). The ages of the males and females nested within each treatment (female-varied, male-varied, and same age) were also significantly different ($F_{42} = 27.69$, $P < 0.0001$). When both males and females were delayed in mating the same number of days, there was an increase in progeny production with 1 and 2 d of delay compared to 0 d of delay, and then progeny production trend downward until 6 d of delay where it stabilized and did not significantly change out to 14 d of delay (Fig. 3A). In contrast, when only one of the sexes was delayed in mating, progeny production had no increase at days 1 and 2, highest progeny production was observed at 0 or 1 d of delay, and the trend was to gradually decrease over time out to 14 d (Fig. 3B and C). With longer periods of mating delay (6 d or more), males have more variation in progeny production than females as progeny production is not consistently reduced as age at mating increased.

There were significant differences depending on whether either sexes were delayed or males or females were delayed (Table 3). When there was no delay in mating, the same-age treatment had fewer progeny than when either only males or only females were delayed. With 1 or 2 d of mating delay, both sexes delayed treatment produced more progeny than either the male delayed or female delayed treatments (except for male delayed on day 1 which was not significantly different from the both sexes delayed treatment). These differences corresponded to the spike in progeny production on days 1 and 2 shown in Fig. 3. With 3–5 d of mating delay, the pattern was reversed with both sexes delayed treatment producing fewer progeny than male or females only delayed, although not significantly different for some comparisons. After 6 d of mating delay, male-only mating delay consistently produced more progeny than either of the treatments where females were delayed in mating the same number of days (Table 3).

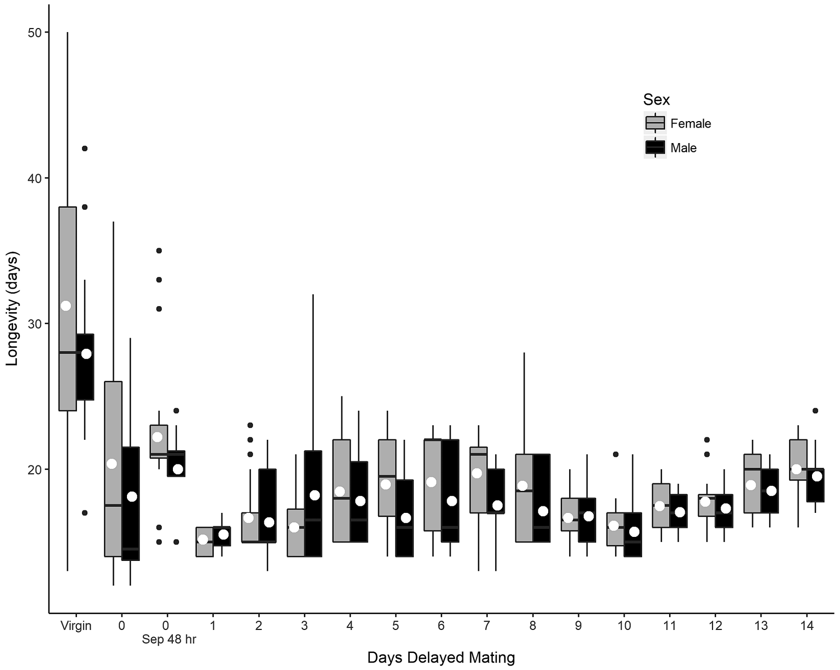

Figure 1. Comparison of the longevity of male and female adult *Lasioderma serricorne*. Longevity was observed for virgin adults, same-age adults (0–14-d old) paired, and 0-d adults that were separated 48 h after they were paired up (0 sep. 48 h). White dot and black line represent the mean and the median, respectively, for any set of data.

Table 2. Mean longevity (in days) of mated and unmated *Lasioderma serricorne* males and females delayed from mating for the same amount of time (0–14 d)

	Females		Males	
Age at mating (days)	Mean longevity (days)	Tukey grouping	Mean longevity (days)	Tukey grouping
Control, unmated	31.2	A	27.9	A
0, separated after 48 h	22.2	B	20.0	B
0, kept together	20.4	BC	18.1	BCD
1	15.2	D	15.5	D
2	16.7	CD	16.4	CD
3	16.0	CD	18.2	BCD
4	18.5	BCD	17.8	BCD
5	19.0	BCD	16.7	BCD
6	19.1	BCD	17.8	BCD
7	19.7	BCD	17.5	BCD
8	18.9	BCD	17.1	BCD
9	16.7	CD	16.8	BCD
10	16.1	CD	15.7	D
11	17.5	CD	17.1	BCD
12	17.8	BCD	17.3	BCD
13	18.9	BCD	18.5	BCD
14	20.0	BC	19.5	BC

Means followed by different letters are significantly different within each sex (Tukey's honest significant difference test, $P < 0.05$). $n = 20$.

Estimating Life History Tables and Net Reproductive Rate, R_o

For the same-age treatment, there was a general decline in R_o as the age at mating increased, although it was not consistent (Fig. 4A). A delay of 13 and 14 d had the lowest R_o values and a delay of 2 d had the highest R_o value, which was significantly different from all other days of delay. For female-varied beetles, there was a similar pattern of decline in R_o as the age at mating increased but again, did not consistently decline as the age at mating increased. A delay of 0 d had the highest R_o value and 14 d of delay again had the lowest R_o value and was significantly different than all other days of delay (Fig. 4B). For male-varied beetles, R_o significantly declined as age at mating increased, although the decline was not consistent throughout the incremental ages and there was considerable overlap in CI among days up through 13 d of delay (Fig. 4C). Mating delay of 14 d had the lowest R_o and was significantly different from all other mating delays imposed (0–13 d). A delay of 8 d in males had the highest R_o value and was significantly different than all other days, followed by a delay of 0 d. Overall, the lowest R_o values were recorded for the longest days of mating delay (11–14 d) for all experiments (Fig. 4).

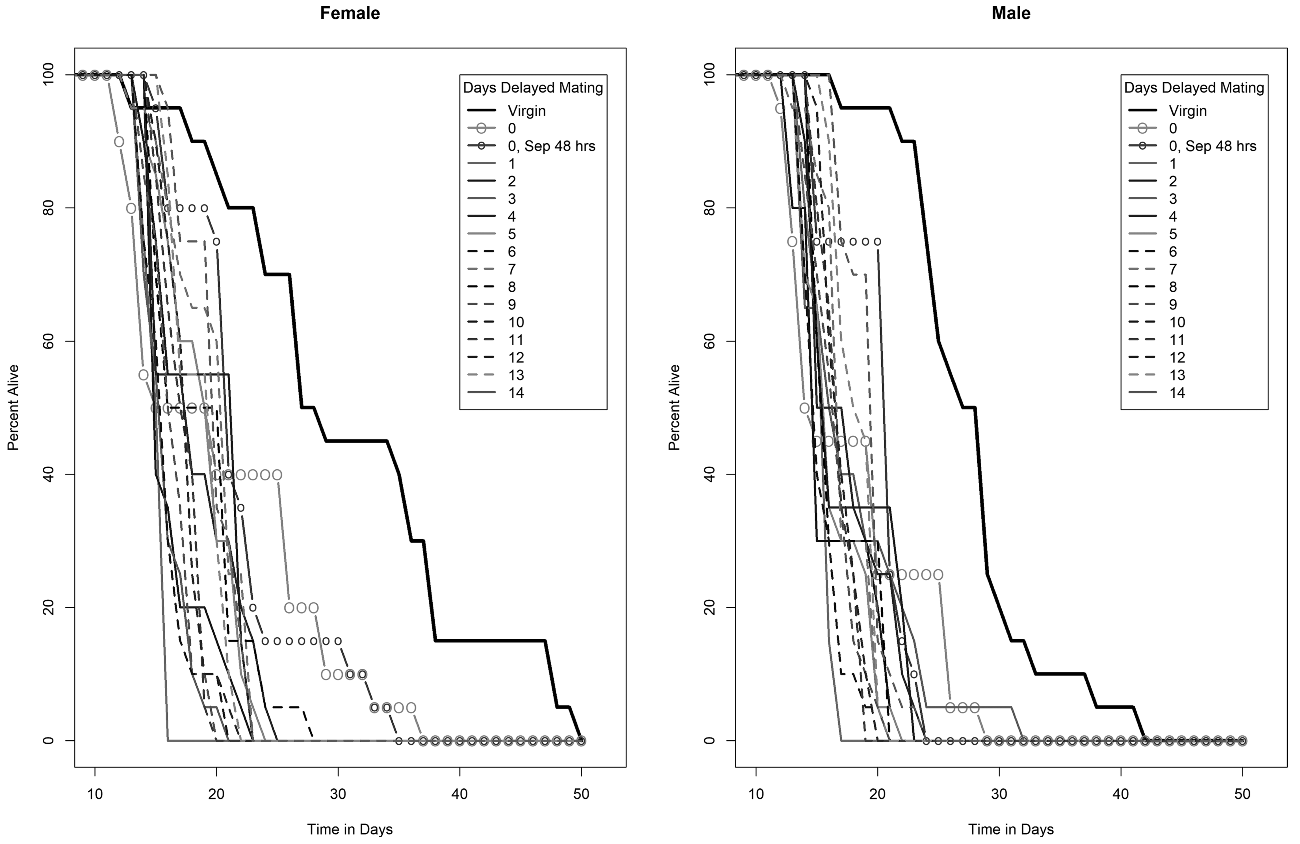

Figure 2. Survivorship of male and female adult *Lasioderma serricorne*. Survivorship is recorded over time for virgin adults, same-age adults (0–14-d old) paired, and 0 d adults that were separated 48 h after they were paired up (0 sep. 48 h). Dashed lines are for delays of 7 d and greater.

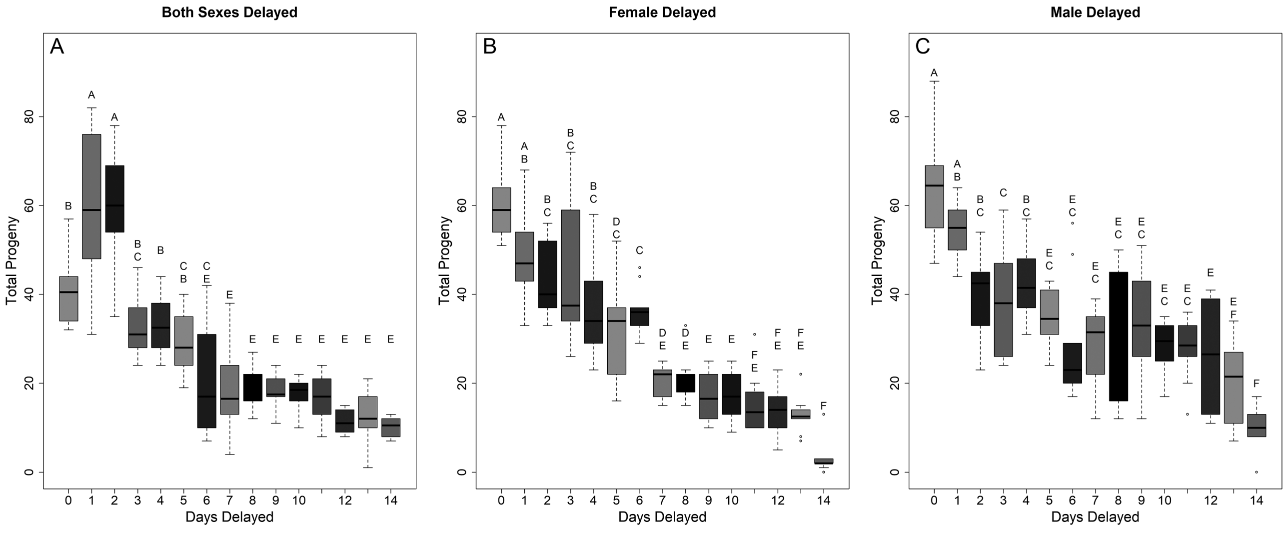

Figure 3. Progeny production in adult *Lasioderma serricorne* delayed from mating for different days. Mating delay was imposed on (A) adults simultaneously—0–14-d-old males and females of the same age were paired, (B) females only—0-d-old males were mated with 0–14-d-old females, and (C) males only—0-d-old females were mated with 0–14-d-old males. Letters on each graph indicate means that are significantly different within each mating delay treatment (Tukey's honest significant difference test, $P < 0.05$).

Discussion

Our results presented here support the hypothesis that mating delay is a crucial factor affecting progeny production. In addition, mating impacted longevity, however, there was less of a consistent pattern between increased mating delay and increased longevity. Findings in the current study are similar to those obtained by Yu (2008), who reported that mated *L. serricorne* adults lived for 17–23 d, while unmated adults lived for 29–35 d. In the current study, unmated adults lived significantly longer (29.6 d) than adults that were mated at 0–14 d of age (15.3–21.1 d). Virgin *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae) and *Sitophilus oryzae* (L.) also lived longer than mated adults of the same age (Singh and

Table 3. LS-means estimates (df = 396, SE = 2.8751) of *Lasioderma serricorne* progeny from the nested model when both males and females were delayed in mating (both sexes mating delayed), when only females were delayed in mating (female mating delayed), or only males were delayed in mating (male mating delayed)

Days mating delayed	Both sexes mating delayed	Female mating delayed	Male mating delayed
0	41.2a	60.1b	63.2b
1	57.8b	48.9a	54.6ab
2	59.1b	44.7a	39.8a
3	32.7a	43.6b	37.8a
4	33.2a	37.2ab	42.4b
5	29.2a	36.1b	34.9ab
6	19.7a	32.2b	28.4b
7	18.9a	20.5a	28.4b
8	19.1a	20.5a	27.8b
9	17.8a	17.6a	32.9b
10	17.7a	17.1a	28.1b
11	16.7a	15.2a	27.8b
12	11.3a	13.7a	26.2b
13	12.5a	12.8a	19.5b
14	10.2b	3.1a	9.3b

Means with different letters indicate independent 95% CI of experiments within days mating delayed (a row).

Wilbur 1966). An increase in longevity of the unmated adults typically occurs because the energy and resources associated with reproduction have a significant fitness cost. The lifespan of insects may be prolonged by reabsorption of nutrients that may have been underutilized in reproduction (Wenninger and Averill 2006). However, for *L. serricorne*, longevity was similar whether females mated on day 0 or day 14. The only treatment that appeared to increase longevity relative to mating at day 0 is if mating pairs were separated after 48 h, which suggests negative fitness effects due to continuous exposure to males after initial mating. This was similar to the findings of Campbell (2005) that showed increased longevity and progeny production in *S. oryzae* when females were separated from males after first mating. This prolonged lifespan may be an indication that multiple matings or attempted matings were occurring and the associated fitness and time costs negatively affecting the longevity (Campbell 2005, Wu et al. 2018). It was also found that female *L. serricorne* live longer than males irrespective of their mating status or their age at mating, but we could not conclude that longevity is more affected by mating delay in one sex than the other as was concluded in other studies (e.g., Singh and Wilbur 1966, Wu et al. 2018). Gerken and Campbell (2018) found for two stored product pest *Trogoderma* species that delaying time to mating increased longevity. Ellis and Steele (1982) also found that virgin females of the African cotton leafworm, *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) and mated females delayed longest from mating (8 d) both lived longest as compared to others that were delayed less time. In female pink bollworm (Lepidoptera: Gelechiidae), the longest mating delays of 10 and 15 d resulted in longevities similar to that of virgins (Lingren et al. 1988).

The age of an insect at mating has been reported to be a crucial factor affecting its reproductive output (Coffelt 1975, Mbata 1985, Makee and Saour 2001, Huang and Subramanyam 2003, Gerken and Campbell 2018, Wu et al. 2018). Coffelt and Burkholder (1973) found that only 5% of 12–16-h-old female *L. serricorne* mated with males and none of the mated females were inseminated. Coffelt and Burkholder (1973) concluded that female cigarette beetles younger than 10 h are not receptive to male copulatory attempts due to sexual immaturity. Although they may be paired up, newly emerged adults may not mate immediately and therefore, may not disburse resources to reproduction until a few days later. We also found that the critical period for *L. serricorne* mating is 1–2 d after emergence and resources necessary for mating may be allocated at an optimal level at this time period. Female cigarette beetles that were mated with delays longer than 1–2 d showed a trend in increased lifespan with decreased progeny production, again suggesting that resources may have been allocated to lifespan when mating is delayed after this critical period. For adult tobacco cutworm, *Spodoptera litura* Fabricius (Lepidoptera: Noctuidae), a day after emergence is very important for its reproductive output, after which reproductive output decreased (Wu et al. 2018). Reproductive output in *T. variabile* and *T. inclusum* decreased with increasing age at mating but peaked at 3 or 4 d after emergence (Gerken and Campbell 2018). In *L. serricorne*, progeny production declined as the age at first mating increased. Our findings suggest that the age at mating may affect the number of successful matings which may subsequently affect the number of progeny produced (Coffelt and Burkholder 1973, Huang and Subramanyam 2003). Also, factors such as the retention of eggs in ovaries in females delayed from mating may contribute to the reduction in progeny production (Mbata 1985). In addition, for all delayed mating experiments, progeny production of *L. serricorne* after 6 d of delay did not vary significantly from each other. To make up for increasing days in delayed mating, *L. serricorne* may also increase the rate of oviposition particularly after 6 d delay. However, this trend is not consistent with other reports that suggest that oviposition rate is similar regardless of when females are mated (Vickers 1997). Further research may be required to determine the specific timing of oviposition in *L. serricorne* as this may be important in developing control strategies.

Multiple mating is common in *L. serricorne* (Coffelt 1975, Levinson and Levinson 1987) with over 90% of males and females mating at least six times and twice, respectively (Coffelt 1975). However, the frequency of mating in *L. serricorne* may have a negligible effect on female fecundity, while female weight and age will have a greater effect (Coffelt 1975). Nonetheless, about 85% of progeny develops from sperm obtained at the second mating (Coffelt 1975), suggesting that a single mating may not provide adequate sperm to fertilize all eggs laid in the lifetime of female *L. serricorne*. Studies in various insect species have shown increased fecundity in some multiple-mated females, and therefore increases in progeny production may be due to the repeated transfer of some compounds including nutrient secretions and other hormones from the male to the female during copulation (Benz 1969, Henneberry and Clayton

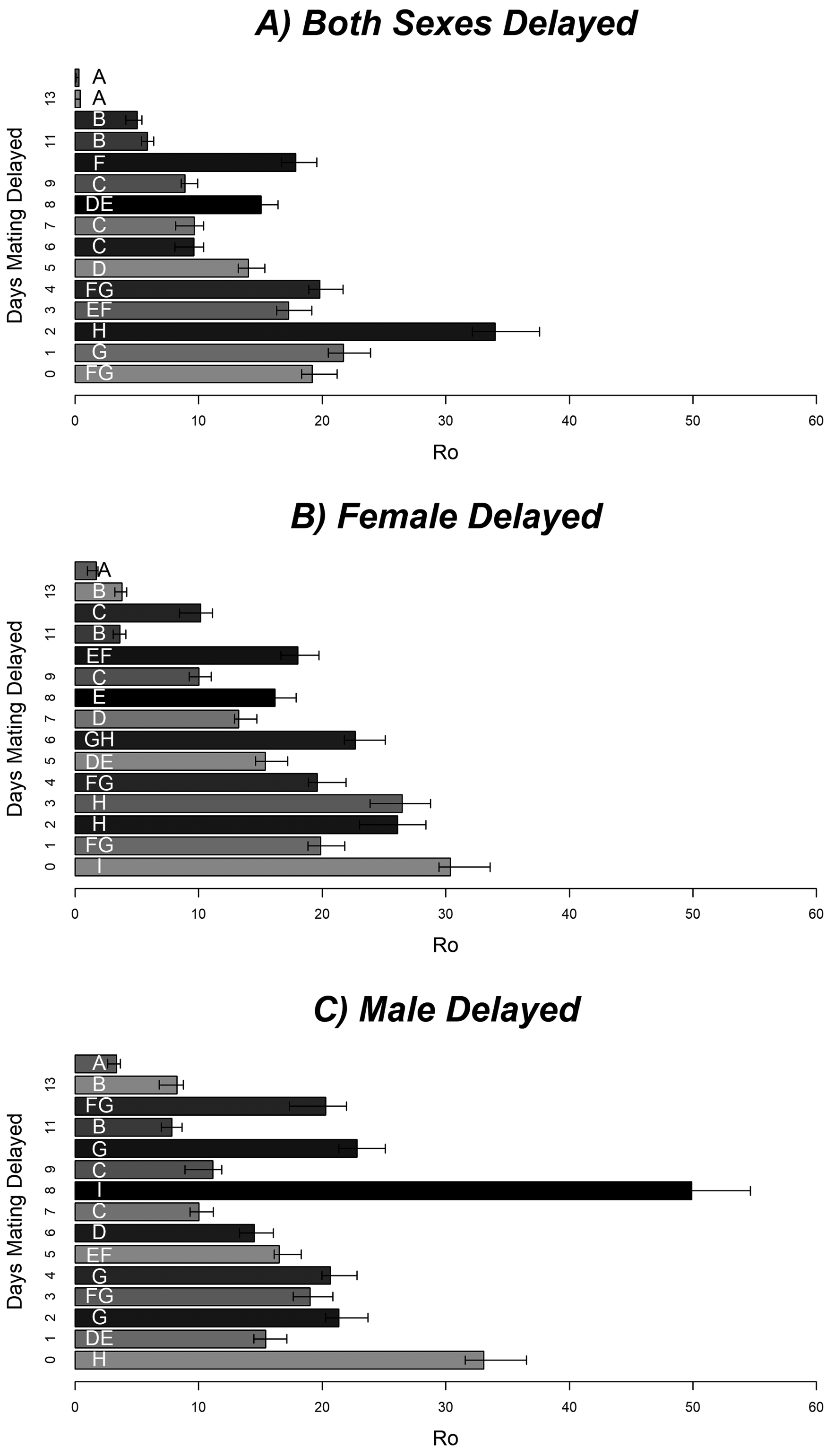

Figure 4. Estimation of net reproductive rate for *Lasioderma serricorne* mated at different ages. Mating delay was imposed on (A) adults simultaneously—0–14-d-old males and females of the same age were paired, (B) females only—0-d-old males were paired with 0–14-d-old females, and (C) males only—0-d-old females were paired with 0–14-d-old males. Graphs with different letters represent means that are significantly different at a 95% CI within each of the three experiments.

1984, Ramaswamy et al. 1997, Park et al. 1998, Campbell 2005). However, multiple mating with multiple males (polyandry) may have a negative effect on progeny production in the female, because of factors including physical harassment from the males (Campbell, 2005). Nonetheless, females may receive genetic benefits to their offspring through multiple mating (Baer and Schmid-Hempel 1999, Tregenza and Wedell 2002).

In the current study, delaying mating by increasing the ages of the adults when they mated causes a marked reduction in progeny production. The effect of a delay in mating on reproduction was greatest for females only, followed by both sexes delayed and then males only having the least effect on progeny production. Female age, therefore, has the greater influence on fecundity. This phenomenon is consistent with reports for other insect species (Torres-Vila et al. 2002, Wu et al. 2018). In some insects, mating delay imposed on both sexes simultaneously was more detrimental to female fecundity than delaying either sex alone (Stelinski and Gut 2009, Wu et al. 2018). Studies in some Lepidopteran pests suggested that this may be because of a decrease in the number of spermatophores transferred by males, decreased egg production, and inadequate sperm quality (Stelinski and Gut 2009, Kawazu et al. 2014). Sex pheromone production by female *L. serricorne* increases with days of emergence and the subsequent attraction of a male has been reported to increase rapidly during the first few days, reaching a maximum at 4–5 d of age (Coffelt and Burkholder 1972). Corresponding to this, maturation of the oocytes does not occur during the pupal stage but requires a period of 3–5 d after the final molt (Howe 1957). Although insects may have been paired soon after emergence in our experiments, successful mating may not have occurred until after some days (Coffelt and Burkholder 1972).

Although not consistent with increasing age, R_o declines as age at mating increased in female mating delay, male mating delay, or both sex mating delay adults, especially 11–14 d delay. Our findings are similar to those obtained in other studies which reported that the R_o of *L. serricorne* vary significantly depending on the age at mating (Nischala and Hari Prasad 2017, 2018) and the food sources on which the insect is raised (Mahroof and Phillips 2008; Saleh 2012; Nischala and Hari Prasad 2017, 2018). Nischala and Hari Prasad (2017) reported R_o ranging from 21.7 to 51.4 for *L. serricorne* reared on different varieties of dry turmeric. In their study, the authors used 2–9-d-old adults, presumably paired same-age adults. Similarly, Nischala and Hari Prasad (2018) studied *L. serricorne* on different varieties of dry ginger and reported lower R_o values ranging from 14.2 to 40.1. In both studies, the authors reported a decline in R_o with increasing age at mating. According to Saleh (2012), the R_o for female *L. serricorne* raised on chicken stock powder, baker's yeast, milo grain, dried ficus, and dried tobacco leaves was 47.5, 42.1, 31.8, 32.6, and 6.0 respectively. In another study, Mahroof and Phillips (2008) mated 0–24-h-old adult *L. serricorne* for 3 d and reported fecundity ranging from 5.8 eggs/female on cigar tobacco, the least acceptable food source among the materials tested, to 52.4 eggs/female on wheat flour, the most preferred. In the current study in which 0–14-d-old adults were used, we reported R_o values that ranged from 0.8 to 35 in same-age adults, 1.6–30 in female delayed mating, and 3.3–51.5 in male delayed mating. These effects of diet and mating delay on fecundity separately, suggest that there could be important effects for the facility and the food materials available on effectiveness of mating disruption programs. Techniques need to be in place to delay mating for 6 d or more, in order for the R_o and subsequent number of progeny to be reduced significantly, reducing the size of subsequent generations.

In addition to age at mating (Coffelt 1975, Mbata 1985, Makee and Saour 2001, Huang and Subramanyam 2003), many other factors including diet, weight, temperature, and light have been shown to be important in determining the fecundity of an insect (Coffelt 1975; Mbata 1985; Shinoda and Fujisaki 2001; Mahroof and Phillips 2008; Vukajlović and Pešić 2012; Saleh 2012; Nischala and Hari Prasad 2017, 2018). Some of these factors may have to be investigated to help develop mating disruption strategies as an alternative control method in managing *L. serricorne*. Findings from our study indicate that a delay in mating significantly reduces reproductive performance. Although a reduction in their reproductive performance may not be reduced to levels that may result in their control, combining mating disruption with other management methods may cause a significant reduction in the population size of subsequent generations.

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