Reproductive Performance of *Tribolium castaneum* (Coleoptera: Tenebrionidae) Exposed to the Minimum Heat Treatment Temperature as Pupae and Adults

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ABSTRACT Managing stored-product insect pests by heating the ambient air of a food-processing facility to high temperatures (50–60°C), also referred to as heat treatment, is an effective technology that has been used since the early 1900s. The minimum temperature during heat treatment for effective disinfestation is 50°C. The effect of sublethal exposures to 50°C on the reproductive performance of stored-product insects associated with food-processing facilities is unknown. The red flour beetle, *Tribolium castaneum* (Herbst), is a pest commonly found in food-processing facilities worldwide. The adverse effects on fecundity, egg-to-adult survival, and progeny production of *T. castaneum* exposed as 1-d-old pupae and 2-wk-old adults to 50°C for 60 and 39 min, respectively, were determined in the laboratory. Pupae and adults exposed for the same time periods at 28°C served as the control treatment. Four possible reciprocal crosses were carried out among adults from the heat-treated (50°C) and control (28°C) treatments. The number of eggs produced during the first 2 wk of adult life, survival of these eggs to adulthood, and adult progeny production after 2 and 8 wk of oviposition in treatments representing all four reciprocal crosses were determined. Fecundity, egg-to-adult survival, and adult progeny production decreased by 17–63, 52–63, and 66–78%, respectively, when males, females, and both males and females were exposed to 50°C. These effects were relatively more pronounced in treatments in which pupae were exposed to the high temperature compared to adults, and in exposed females than in males. The impaired reproductive performance in *T. castaneum* pupae and adults surviving sublethal exposures to the minimum heat treatment temperature is valuable for understanding population rebound following a heat treatment intervention.

KEY WORDS methyl bromide alternative, heat treatment, *Tribolium castaneum*, reproductive impairment

METHYL BROMIDE IS A WIDELY used structural fumigant for managing stored-product insects in food-processing facilities. Concerns about methyl bromide's stratospheric ozone-depleting effects (Makhijani and Gurney 1995) may result in its phaseout by the year 2005 in the United States (Anonymous 1992, 1993). Several techniques are being considered as possible alternatives to methyl bromide. One such alternative is the use of high temperatures, or heat treatment, a technology that is well known to the food industry for >80 yr (Dean 1911, 1913). Heat treatment involves raising the temperature of the ambient air within a facility, or a portion of it, to 50–60°C and holding these temperatures for 24–36 h to kill stored-product insects (Fields 1992; Dowdy 1999; Dowdy and Fields 2002; Wright et al. 2002; Mahroof et al. 2003a, b; Roesli et al. 2003). The major challenge with heat treatment is nonuniform distribution of the heated air caused by temperatures stratifying both horizontally and vertically within the heated facility (Dowdy 1997, Mahroof et al. 2003a). Thus, some portions of the facility may be overheated (>60°C), whereas other portions may be underheated (<50°C) (Dowdy 1999, Mahroof et al. 2003a). This results in inefficient use of the generated heat and the potential development of two undesirable conditions. First, overheating an area may result in damage to processing equipment or damage to the building's structural integrity. Second, underheating an area may result in survival of insects because of exposure to a sublethal temperature or exposure to lethal temperature for less than the intended duration (sublethal exposure). Several researchers have shown that insects surviving sublethal exposures to a lethal temperature may have impaired fecundity, fertility, and development (Proverbs and Newton 1962, Okasha et al. 1970, Gonen 1977, Arbogast 1981, Tikku and Saxena

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1985, Kawamoto et al. 1989, Tikku and Saxena 1990, Saxena et al. 1992, Lale and Vidal 2003).

Exposure to a sublethal temperature (44°C) was effective in producing either partial or complete sterility of the confused flour beetle, *Tribolium confusum* Jacquelin du Val, exposed as larvae or pupae (Oosthuizen 1935). For example, only 1.3% of the eggs laid by females hatched when the females were exposed as pupae of *T. confusum* for 8 h to 44°C and 75% RH. But the egg hatchability was 11% when month-old virgin adult females were exposed to 44°C and 75% RH and crossed with males. Saxena et al. (1992) reported that high temperature adversely affected reproduction of three stored-product insect pests. When the khapra beetle, *Trogoderma granarium* Everts, pupae were exposed for 48–72 h to 45°C, the adults emerging from pupae were incapable of propagating a new generation because of complete mortality of larvae hatching from eggs laid by the adults. When 1-, 2-, or 3-d-old pupae of the red flour beetle, *Tribolium castaneum* (Herbst), were exposed to 45°C for 48 or 72 h, development of the subsequent generation was completely suppressed because larvae failed to complete development to the pupal stage. When 2- or 3-d-old pupae of *T. castaneum* were exposed to 45°C for 48 h, adult progeny emerging from pupae failed to produce any larvae during a month-long observation period. When 1-d-old pupae were exposed to 45°C for 24 h, however, an average of 40 live larvae were found after 1 mo, but no larvae were found if 1-d-old pupae were exposed to 45°C for 48 or 72 h. Saxena et al. (1992) also showed that exposing 2- or 3-d-old pupae of the Southern cowpea weevil, *Callosobruchus chinensis* L., to 45°C for 48 or 72 h significantly affected egg laying and hatching. No eggs were produced when pupae were exposed to 45°C for 48 h. The review by Gonen (1977) cited that 2-wk-old adult females of the granary weevil, *Sitophilus granarius* (L.), exposed to 35°C for 7 d and subsequently reared at 26.5°C showed a 97% reduction in the number of adult progeny produced, compared with that of females reared at 26.5°C. Arbogast (1981) reported that when the almond moth, *Cadra cautella* (Walker), male pupae were exposed to 45°C for 2 h and paired with unexposed virgin females, an average of 304 eggs per female were laid. When heat-treated female pupae were paired with a normal virgin male, however, an average of 153 eggs per female was laid. Thus, the magnitude of adverse effect of high temperature on reproduction in *C. cautella* seemed to be more severe in exposed female pupae than in male pupae.

Most of the work on of the reproductive effects of high temperatures on *T. castaneum* was conducted at temperatures ≤45°C. During heat treatment, the minimum temperature for effective disinfestations should be at least 50°C (Wright et al. 2002; Mahroof et al. 2003a, b; Boina and Subramanyam 2004). Very little is known about the possible reproductive effects on stored-product insects surviving short exposures (sublethal exposures) to the temperatures used during heat treatments. Our aim was to find out whether sterility is induced in survivors exposed to 50°C. Therefore, laboratory experiments were designed to quantify the effects of 50°C on the fecundity, fertility, and progeny production of *T. castaneum* exposed as pupae and adults. We selected *T. castaneum* because it is an economically important pest associated with food-processing facilities worldwide (Sinha and Watters 1985, Mills and Pedersen 1990).

Materials and Methods

Insect Stages and Temperature. Pupae and adults of *T. castaneum* used in the experiments were from cultures maintained in the Department of Grain Science and Industry's Stored-Product Laboratory since 1999. Voucher specimens (no. 159) of the red flour beetle used in the experiments are located in the Kansas State University Museum of Entomological and Prairie Arthropod Research. Pupae that were a day old and adults that were 2-wk-old were used in experiments at 50°C. We used 1-d-old pupae because the onset of sexual maturity in *T. castaneum* takes place during the early pupal period (Sokoloff 1974). Thus, the adverse effects of high temperature on the reproductive system may be more pronounced if pupal stages are exposed to high temperatures. Adults were used in tests because, in food-processing facilities, this stage is normally the most visible and active, is capable of flying, and can potentially escape the lethal effects of high temperatures. The 50°C temperature was used because it is the minimum desired temperature during heat treatments. Temperatures above 50°C were not examined in the current study because of significant and rapid mortality of *T. castaneum* stages (Mahroof et al. 2003b).

Sexing *T. castaneum* Pupae. Adults of *T. castaneum* were reared in a growth chamber (model I-36 VL, Percival Scientific, Perry, IA) at 28°C, 65% RH, and a photoperiod of 14:10 (L:D) h on 95% bleached wheat flour and 5% (by weight) powdered brewer's yeast. Eggs were collected every 24 h from adult cultures and were transferred to separate 30-ml plastic cups with cardboard lids. Each cup held a mean ± SE of 5.1 ± 0.1 g ($n = 10$) of whole-wheat flour and brewer's yeast in the same ratio as described previously. Three eggs of *T. castaneum* were introduced into each cup, and the eggs were reared at the conditions previously described. Insect stages in plastic cups were monitored daily for pupation, and any live *T. castaneum* pupae were sexed within 8 h of pupation. Sexing was done by separating pupae from the medium and by examining their external genitalia under a stereomicroscope (Nikon SMZ 645) according to a standard method (http://bru.gmprc.ksu.edu/proj/tribolium/wrangle.asp). After sexing, male and female pupae were placed in separate 0.45-liter glass jars at 28°C and 65% RH until they were used in the experiments.

Insect Exposure to 50°C and Reciprocal Crosses. The time for 50% survival of insects (LT_{50}) was used to ensure availability of sufficient insect numbers for studying reproductive effects. Pupae and adults were exposed to 50°C and 25% RH in a growth chamber for 60 and 39 min, respectively. These exposure times are

known to result in 50% survival of insects (Mahroof et al. 2003b).

Immediately after sexing, 1-d-old male and female pupae were transferred to separate square plastic boxes (4.5 by 4.5 by 1.5 cm) with perforated lids covered with 600-μm-opening wire mesh screens. Each box held ≈305 mg of bleached wheat flour and 100 male or female pupae. Ten such boxes for each sex were exposed to 50°C and 25% RH for 60 min. An additional time of 8 min was allowed for the flour in the boxes to reach to the set chamber temperature of 50°C, based on our observations from a previous study (Mahroof et al. 2003b). At the end of the exposure, all boxes were transferred back to the chamber at 28°C, 65% RH, and a photoperiod of 14:10 (L:D) h. The control treatment consisted of 10 separate boxes, each holding 100 male or 100 female pupae, exposed to 28°C and 65% RH. Three days after exposure to 28 or 50°C, boxes were examined for live and dead pupae. Pupae that turned black were considered dead, and were discarded.

Reciprocal crosses were carried out with adults emerging from heat-treated (50°C) and control (28°C) pupae: a control female crossed with a control male, a control female crossed with a heat-treated male, a heat-treated female crossed with a control male, and a heat-treated female crossed with a heat-treated male. Each adult pair was placed in a 30-ml plastic cup with a cardboard lid, holding 5.1 g of the culture medium. After pairing, all plastic cups were maintained at 28°C, 65% RH, and a photoperiod of 14:10 (L:D) h. Fifteen subsamples were maintained for each reciprocal cross. The entire experiment was replicated three times.

To obtain 2-wk-old adults, pupae were sexed and placed in 0.45-liter glass jars with 60 g of the culture medium at 28°C, 65% RH, and a photoperiod of 14:10 (L:D) h. One hundred male and female adults were introduced into separate plastic boxes (4.5 by 4.5 by 1.5 cm) with 305 mg of whole wheat flour. Ten boxes for each sex were exposed to 50°C for 39 min, after accounting for the time taken for flour to reach set chamber temperature (8 min). After 50°C exposure, all boxes were transferred back to the chamber maintained at 28°C. The control treatment consisted of 2 wk old adults in boxes exposed for 47 min at 28°C and 65% RH. All adults exposed to 28 and 50°C were held for 24 h at 28°C, 65% RH, and a photoperiod of 14:10 (L:D) h to separate live and dead adults. Immobile adults were considered dead. A pair of live male and female adults was transferred to an individual plastic cup holding 5.1 g of the culture medium.

Measuring Fecundity. The number of eggs laid by females after pairing was determined by counting eggs laid weekly, for two consecutive weeks. Each week, the adult pair was gently removed from the cup. The flour in the cup was sifted over a sieve with 250-μm openings. The eggs retained on the sieve were transferred to a glass petri dish and counted under a stereomicroscope. After the first week, the adults in the pair were transferred to a new plastic cup with fresh culture medium and were maintained at 28°C, 65% RH, and a photoperiod of 14:10 (L:D) h for another week. At the end of the second week, the number of eggs laid was counted. The total number of eggs laid in 2 wk was averaged across the 15 subsamples of a replicate.

Egg-to-Adult Survival. All eggs laid within 2 wk in each pair as described above were reared to adulthood at 28°C, 65% RH, and a photoperiod of 14:10 (L:D) h in 150-ml plastic containers holding 40 g of the culture medium. After 4 wk, egg-to-adult survival was calculated from the number of adults that emerged out of the total eggs laid within the 2-wk time period. Egg-to-adult survival in all 15 subsamples was averaged for each replicate.

Progeny Production. Two separate experiments were carried out to test the effect of 50°C on adults in subsequent progeny production. Progeny production was estimated based on two and 8 wk of oviposition in treated insects. Progeny produced at the end of 2 wk will indicate possible short-term adverse effects of high temperature, whereas progeny produced at the end of 8 wk will indicate long-term adverse effects. All possible reciprocal crosses between heat-treated (50°C) and control (28°C) insects were carried out using adults that emerged from 1-d-old pupae or 2-wk-old adults according to previously described protocols. Five male and female pairs (subsamples) from each reciprocal cross within a replicate were transferred to 150-ml plastic containers with 40 g of culture medium and were maintained at 28°C, 65% RH and 14:10 (L: D) h for two or 8 wk. After 2 wk, the original mating pair was discarded, and the immature stages in the flour were reared in the same medium until emergence of adults. Under similar conditions, five mating pairs from each reciprocal cross were directly transferred to 150-ml plastic containers with 40 g of the culture medium. These pairs were examined after 8 wk to count the number of adult progeny produced. These experiments were repeated three separate times. Progeny production in each replicate was determined by averaging values across the five subsamples.

Data Analysis. The experiment was conducted as a randomized complete block, with the reciprocal crosses serving as treatments and replication serving as blocks. Blocks were considered as random effects. Data on the number of eggs laid and adult progeny production were transformed to log $(x + 1)$ scale, whereas percentage egg-to-adult survival data were transformed to arcsine $(x)^{0.5}$ (Zar 1984). Data were subjected to analysis of variance (ANOVA) by using the MIXED procedure of SAS (SAS Institute 1999) to determine significant differences between the stages and treatments in fecundity, egg-to-adult survival, and progeny production. Additionally, ANOVA was performed by stage to determine significant differences among the four reciprocal crosses in fecundity, egg-to-adult survival, and progeny production. Linear contrasts were used for separating treatment means at the $\alpha = 0.05$ level.

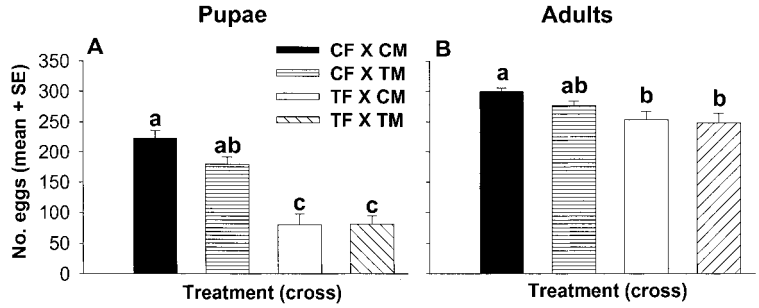

Fig. 1. Number (mean ± SE) of eggs laid in two weeks by *T. castaneum* exposed to 50°C as pupae or adults. Control insects were exposed to 28°C. CF X CM, control female crossed with control male; CF X TM, control female crossed with treated male; TF X CM, treated female crossed with control male; and TF X TM, treated female crossed with treated male. Within a stage, means with different letters are significantly different ($P < 0.05$; linear contrasts).

Results

Effects on Fecundity. There were significant differences between pupae and adults ($F = 124.0$; df = 1, 14; $P < 0.0001$) and among treatments ($F = 18.73$; df = 3, 14; $P < 0.0001$) in the mean number of eggs laid. The interaction of stage and treatment was also significant ($F = 13.71$; df = 3, 14; $P = 0.0002$). Mean number of eggs laid in heat-treated pupae was ≈53% less than that of heat-treated adults. There were also significant differences in the mean number of eggs laid in 2 wk among the four reciprocal crosses in experiments with pupae ($F = 17.4$; df = 3, 6; $P = 0.002$) or adults ($F = 6.2$; df = 3, 6; $P = 0.028$). In experiments with pupae, there was a 19% decrease in the mean number of eggs laid when a control female was paired with a heat-treated male compared with the number of eggs laid when a control female was paired with a control male (Fig. 1A). However, the difference between these treatments was not statistically significant ($P > 0.05$). The least number of eggs (80 eggs per female per 2 wk) was laid in crosses in which a heat-treated female was paired with a control male and a heat-treated female was paired with a heat-treated male. Differences between these two treatments were not statistically significant ($P > 0.05$), but they differed significantly ($P < 0.05$) from treatments in which a control female was paired with a heat-treated male (179 eggs per female per 2 wk) and a control female was paired with a control male (222 eggs per female per 2 wk). A similar trend among treatments was observed in experiments with 2-wk-old adults (Fig. 1B), but the magnitude of differences among the four reciprocal crosses was smaller, compared with experiments involving pupae. Differences among the treatments having either heat-treated males, heat-treated females, or heat treated males and females were not significantly different from one another ($P > 0.05$).

Egg-to-Adult Survival. There were significant differences between stages ($F = 4.8$; df = 3, 14; $P = 0.046$) and among treatments ($F = 27.2$; df = 3, 14; $P < 0.0001$) in the mean percentage of egg-to-adult survival. The stage and treatment interaction was not significant ($F = 0.42$; df = 3, 14; $P = 0.7391$), indicating that the differences among the treatments were consistent for each stage. The mean egg-to-adult survival in heat-treated pupae was 9% less than that of heat-treated adults. The mean egg-to-adult survival was significantly different among treatments in experiments with pupae ($F = 8.4$; df = 3, 6; $P = 0.014$) or adults ($F = 103.1$; df = 3, 6; $P < 0.0001$). The mean survival rate of unexposed (control) pupae was ≈83%, and was significantly different ($P < 0.05$) from the 37–42% survival rates observed in the other three reciprocal crosses (Fig. 2A). Trends in the egg-to-adult survival rate in experiments with 2-wk-old adults were similar to those observed for pupae (Fig. 2B). Although the fecundity was not different in the treatment where a control female paired with a heat-treated male compared with that of a control female paired with a control male, the egg-to adult-survival rate was significantly reduced ($P < 0.05$) in the former treatment compared with the latter.

Adult Progeny Production. There were no significant differences between stages ($F = 3.24$; df = 3, 32; $P > 0.081$) in the mean number of adult progeny produced, but significant differences were found among treatments ($F = 3505$; df = 3, 32; $P < 0.0001$) and between the two time periods ($F = 92.1$; df = 1, 32; $P < 0.0001$). Except for the stage by treatment interaction ($F = 6.11$; df = 3, 32; $P < 0.002$), the stage by time ($F = 1.26$; df = 1, 32; $P > 0.27$), treatment by time ($F = 2.62$; df = 3, 32; $P > 0.068$), and stage by treatment by time ($F = 0.78$; df = 3, 32; $P > 0.517$) interactions were not significant. Significant differences were found in the mean number of adult progeny produced after 2 wk of oviposition among the four reciprocal crosses in experiments with pupae ($F = 101.1$; df = 3, 6; $P = 0.009$) or adults ($F = 32.02$; df = 3, 6; $P < 0.0001$). Progeny production in a control female paired with a heat-treated male and a control female paired with a control male in experiments with pupae were significantly different from one another ($P < 0.05$), with a 54% reduction in progeny production in the former treatment compared with the latter (Fig. 3A). Progeny production was similar ($P > 0.05$) between treatments in which a heat-treated female

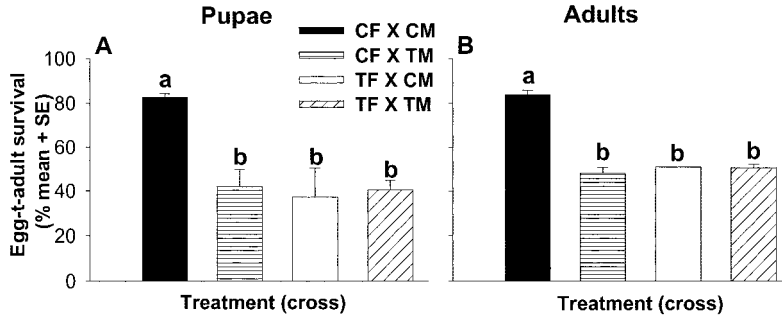

Fig. 2. Percentage (mean ± SE) of adults that developed from eggs laid within 2 wk by *T. castaneum* exposed to 50°C as pupae or adults. Control insects were exposed to 28°C. CF X CM, control female crossed with control male; CF X TM, control female crossed with treated male; TF X CM, treated female crossed with control male; and TF X TM, treated female crossed with treated male. Within a stage, means with different letters are significantly different ($P < 0.05$; linear contrasts).

was paired with a control male (37 adults) and a heat-treated female was paired with a heat-treated male. However, progeny production in these two treatments was significantly less ($P < 0.05$) than that in the treatment in which a control female was paired with a control male.

Experiments with adults (Fig. 3B) showed a significant reduction ($P < 0.05$) in the number of adult progeny produced in all treatments in which one of the sexes was heat treated, compared with production in the control treatment where both sexes were untreated. The magnitude of reduction in progeny production observed with heat-treated adults was smaller than the reduction observed with heat-treated pupae.

There were also significant differences in the mean number of adult progeny produced after 8 wk of oviposition among the four reciprocal crosses in experiments with pupae ($F = 2846.8$; df = 3, 6; $P < 0.0001$) or adults ($F = 126.8$; df = 3, 6; $P < 0.0001$). Experiments with pupae showed that all four reciprocal crosses were significantly different ($P < 0.05$) from each other (Fig. 3C). The largest number of adult progeny (244 adults) was produced in the control female × control male treatment, whereas the smallest number of adult progeny (53 adults) were produced in the heat-treated female × heat-treated male treatment. The progeny production trend after 8 wk in experiments with adults was similar to that observed in experiments with pupae (Fig. 3D) with one exception. There was a 14% reduction in adult progeny production that was significant ($P < 0.05$) in the control female × heat-treated male treatment compared with production in the heat-treated female × control male treatment.

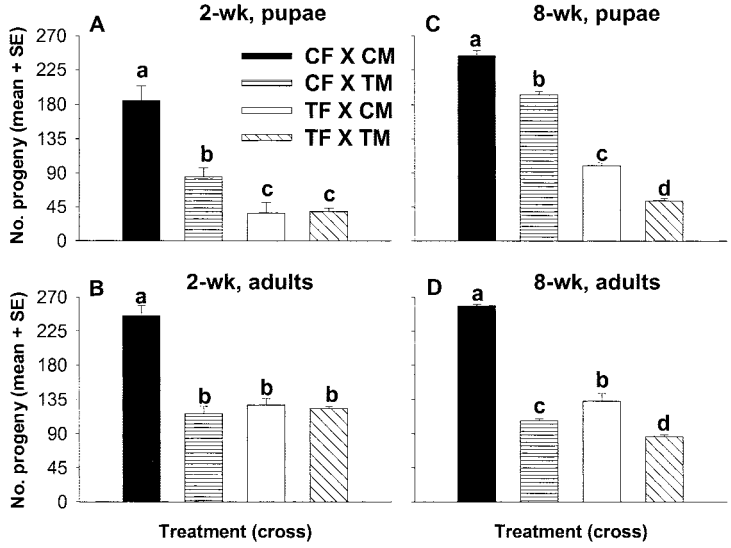

Fig. 3. Number (mean ± SE) of adult progeny produced from eggs laid by *T. castaneum* within 2 and 8 wk in experiments with pupae or adults exposed to 50°C. Control insects were exposed to 28°C. CF X CM, control female crossed with control male; CF X TM, control female crossed with treated male; TF X CM, treated female crossed with control male; and TF X TM, treated female crossed with treated male. Within a stage and treatment time, means with different letters are significantly different ($P < 0.05$; linear contrasts).

Discussion

Exposure of *T. castaneum* pupae or adults to 50°C adversely affected early fecundity, egg-to-adult survival, and adult progeny production. The magnitude of effects observed was consistently greater when exposure occurred in the pupal stage, rather than in the adult stage. Adverse effects of 50°C were greater in experiments with pupae rather than adults because, in *T. castaneum*, ovaries and spermatheca mature mainly during the early pupal period (Sokoloff 1974). Oosthuizen (1935) suggested that sterility in larvae or pupae exposed to high temperatures was caused by abnormal maturation division. Abnormal maturation divisions frequently result in an unbalanced chromatin condition, which, at times, proves to be lethal to the zygote. But whether such abnormal maturation is due to chromosomal fragmentation or cytoplasmic changes is unknown (Oosthuizen 1935). Abnormal cell divisions may result in defective spermatozoa. Defective sperm are produced at high temperatures because of the inability of the sperm to separate out due to ensheathment by a common plasma membrane (Saxena et al. 1992).

High temperatures disrupt the normal functioning of the reproductive system in both males and females, but females tend to be more vulnerable in some species. Generally, the adverse effects were greater when females of *T. castaneum* were exposed to 50°C rather than males. Our oviposition studies suggest that males from pupae or adults exposed to 50°C showed no indication of sterility when mated with untreated (control) females. Females from pupae or adults exposed to 50°C showed considerable reduction in the number of eggs laid, egg-to-adult survival, and progeny production when mated to untreated (control) males, revealing only partial sterility. Oosthuizen (1935) reported that exposure of larvae or pupae of *T. confusum* to high temperatures, ranging from 37.5 to 44°C for 24–72 h, produced either partial or complete sterility, depending on the temperature and the length of exposure. Arbogast (1981) reported that when *C. cautella* male and female pupae were exposed to 45°C for 2 h, the magnitude of the adverse effects of high temperature on reproduction was more severe in exposed female pupae than in male pupae. However, in cultures of the fruit fly *Drosophila melanogaster* Meigen, reared at 31°C (Young and Plough 1926), and in *T. granarium* pupae exposed to 45°C for 24–72 h (Saxena et al. 1992), sterility was more pronounced in males than in females. High temperatures are known to depress egg production more readily than sperm production in insects (Chapman 1998), but their precise effect on the male and female reproductive systems is not fully understood.

In the current study, pupae or adults of *T. castaneum* exposed to 50°C showed significant reduction in fecundity. In a related study by Lale and Vidal (2003), females of the cowpea weevil, *Callosobruchus maculatus* (F.), exposed to 50°C for 1 h laid an average of 0.6 eggs within 24 h compared with females exposed to 40°C for 1 h, which laid 14.1 eggs. In the pulse beetle, *Callosobruchus subinnotatus* (Pic), exposure of females to 50°C for 1 h resulted in an average of 1.3 eggs being laid after 24 h (Lale and Vidal 2003). Fecundity in females at this temperature and exposure time was significantly less than fecundity observed after exposure to 40°C for 1 h (six eggs). Lale and Vidal (2003) inferred that the reduced oviposition might have resulted from adverse effects of high temperatures on the reproductive physiology of *C. maculatus* and *C. subinnotatus.* Noda and Saito (1979) reported that exposing 6-d-old nymphs of the brown planthopper, *Laodelphax striatellus* Fallèn, to 40°C for 3 h resulted in adults laying an average of 4.5 eggs per female, whereas normal brachypterous adults laid an average of 11.7 eggs per female. Oosthuizen (1935) reported that temperature may affect egg production by altering the rate of egg formation in the ovary. Destruction of matured egg cells, primary and secondary oocytes, or other heat-related injury to ovarian tubules may affect egg production. Changes in temperature also adversely affect the central nervous system. Changes in nerve function will affect the activity of the endocrine system (Chapman 1998, Denlinger and Yocum 1999). Neven (2000) indicated that many changes in insect reproduction could be due to changes in the endocrine system. Effects on the endocrine system may prevent maturation of germ cells and inhibit deposition of vitellin in the eggs.

Temperatures in excess of the physiological limits for egg hatching, larval development, or eclosion of adults and pupae rapidly increase mortality (Bursell 1974). The temperature of 50°C, which is 10°C higher than the upper physiological limit for *T. castaneum* (Howe 1965), perhaps contributed to the decreased egg-to-adult survival observed. Lale and Vidal (2003) reported a 75% reduction in the number of adults that developed after exposure of *C. maculatus* eggs to 50°C for 1 h. Reduced egg-to-adult survival affects the number of progeny produced. A 6.4-fold reduction in the number of adult progeny was observed when *C. maculatus* females were exposed to 50°C for 1 h, compared with females exposed to 40°C for 1 h (Lale and Vidal 2003). We conducted a progeny production experiment only for a maximum period of 8 wk of oviposition. The main difficulties in conducting experiments with *T. castaneum* are its long adult survival time (several months to a year) and cannibalism (Anonymous 1986).

The results of the current study indicated that a temperature of 50°C reduced fecundity, egg-to-adult survival rate, and adult progeny production of *T. castaneum.* The adverse effects of high temperature on *T. castaneum* reproduction are important for understanding population increases of this pest after a heat treatment. Pest population buildup after a heat treatment partly depends on the reproductive performance of survivors. In our study, food was not a limiting factor for *T. castaneum.* Sanitation of the floor and equipment of a food-processing facility before heat treatment improves effectiveness in killing insects, because food materials are poor conductors of heat and serve to insulate insects from high temperatures.

Therefore, the adverse effects observed in the study may be more pronounced in survivors during an actual heat treatment.

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