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Impact of Mating Frequency on Reproductive Success of *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

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Authors' contributions

This work was carried out in collaboration among all authors. Authors VME and RJS conceptualized the work. Authors RJS, VME and SGS carried out the experiments. Authors SSP and DKN helped in data analysis. Authors RJS and VME wrote, reviewed and edited the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

This study investigates the influence of mating frequency on the reproductive success of *Spodoptera frugiperda*, a significant agricultural pest. We compared the effects of single and multiple matings on fecundity and hatching percentage using laboratory-reared moths. Females subjected to multiple matings exhibited significantly higher fecundity and improved hatching

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success compared to single-mated females. Specifically, multiple-mated females produced an average of 1468.6 eggs with a hatching percentage of 88.8%, while single-mated females produced 858 eggs with a hatching percentage of 78.4%. These results are consistent with the hypothesis that multiple mating provides nutritional and genetic benefits, enhancing reproductive output and offspring viability. The study highlights the role of mating frequency in shaping reproductive performance and suggests potential applications for pest management strategies. By targeting mating behaviors, such as through mating disruption or sterilization, it may be possible to mitigate the impact of *S. frugiperda* on crops. This research contributes to our understanding of the reproductive dynamics of this pest and offers insights for developing more effective pest control measures.

Keywords: Spodoptera frugiperda; mating frequency; fecundity; hatching success; polyandry; pest management.

1. INTRODUCTION

Reproduction in insects is a complex process, influenced by a variety of factors including climate, food availability, and mating behaviors such as frequency and duration [1]. Among these, the frequency of mating plays a crucial role in determining oviposition success, which directly impacts population dynamics [2]. In Lepidoptera, multiple mating, or polyandry, is a widespread phenomenon where both males and females often mate more than once, a behavior observed in field-collected females containing multiple spermatophores [3]. The evolutionary underpinnings of polyandry suggest that males, whose reproductive investment is small, are more likely to engage in multiple matings, as predicted by sexual selection theory [4]. However, factors such as the time needed to replenish spermatophore materials and the quality and mating status of females may influence a male's propensity to remate [5,6].

For females, engaging in multiple matings can offer significant benefits. It may help replenish sperm supplies, ensuring adequate fertilization of all eggs, and can enhance fecundity and longevity through the acquisition of nutrients from males during copulation. Additionally, multiple mating may increase the genetic diversity of offspring, offering a potential evolutionary advantage, and reduce the time and energy females need to resist further copulation attempts [7,8,3]. Furthermore, understanding the dynamics of monandry (single mating) and polyandry (multiple matings) is essential for comprehending mating frequencies and reproductive success, which in turn influence population growth [9,10].

The fall armyworm (*Spodoptera frugiperda* J.E. Smith) (Lepidoptera: Noctuidae) is a highly destructive polyphagous pest native to the tropical and subtropical regions of the Americas. This species is notorious for its substantial egg-laying capacity and remarkable flight abilities. The scientific name *Spodoptera frugiperda* is derived from Latin, meaning "lost fruit," a reference to the significant crop losses caused by its larval stage [11]. Invasive species, like the fall armyworm, often exhibit a strong capacity to adapt to new environments, which is a key factor in their successful spread [12]. Although originally confined to the Americas, the fall armyworm began its invasion into various African countries in 2016, presenting a major threat to agricultural sustainability, particularly in Sub-Saharan Africa. The first confirmed presence of the fall armyworm in India was in maize fields in the southern state of Karnataka in May 2018 [13]. It is highly polyphagous, with a host range of 353 plant species, inflicting significant damage on crops such as sorghum, maize, soybean, and cotton [14,15,16]. In Ghana and Zambia, FAW-induced yield losses range from 22% to 67% [17], translating to annual losses between 4.1 and 17.7 million tonnes across African countries [18]. The pest's ability for long-distance migration and increased globalization has facilitated its spread to new regions [19]. Additionally, its high fecundity, with more than 1000–1500 eggs, and its polyphagous nature contribute to its successful colonization and severe crop damage in new areas [20].

A study by Simmons et al. [21] demonstrated that, based on the number of spermatophores in the bursa copulatrix of mated females, female moths mated an average of 3.7 times. However, the effects of mating frequency on fecundity were not extensively studied. Understanding the reproductive biology of *S. frugiperda* is crucial for developing effective management strategies. Mating behavior plays a pivotal role in fecundity, the potential reproductive capacity of an organism, and the subsequent hatching success of eggs. Previous studies have indicated that mating frequency can significantly influence reproductive outcomes, yet the specific effects of single versus multiple matings on the fecundity and hatching percentage of fall armyworm remain underexplored. This research aims to fill this gap by systematically examining how different mating strategies affect reproductive performance in this pest. The primary objective of this study is to investigate the impact of single and multiple matings on the fecundity and hatching percentage of fall armyworm. By comparing these two mating strategies, the study seeks to provide insights into the reproductive dynamics of *S. frugiperda*, which could have implications for pest management practices. Understanding how mating frequency affects reproductive success will not only enhance our knowledge of the species' biology but also inform strategies for controlling its populations in agricultural settings. This research aims to contribute to the broader field of entomology and pest management by elucidating the relationship between mating behavior and reproductive outcomes in fall armyworm.

2. MATERIALS AND METHODS

2.1 Rearing of Test Insect

The larvae of *S. frugiperda* were reared in the laboratory using baby corn. Pupae were sexed and housed in separate vials until they emerged [22]. The insects were kept under controlled conditions with a photoperiod of 12 hours light and 12 hours dark, at a temperature of 27° ± 1°C, and 65% ± 5% relative humidity (RH) until emergence. The rearing was conducted in the Insect Physiology and Molecular Biology Laboratory, Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi. Once the adults emerged, they were provided with a 10% honey solution on cotton, placed in small Petri dishes. Emergence was recorded as day one, and observations were made over seven scotophases, starting at 1800 hours and ending at 0600 hours.

2.2 Mating Behavior Observation

To study the mating behavior of single-mated and multiple-mated *S. frugiperda* females, transparent plastic jars (17.5 cm height by 10.5 cm diameter) were used in a completely randomized design. Each jar was covered with black muslin cloth to ensure darkness.

2.3 Experimental Setup

Single Mating Treatment: Fifteen pairs of male and female moths (1:1 ratio) were placed in jars. Males were removed after a single mating event, confirmed by dissecting the females to identify a single spermatophore in the bursa copulatrix after its death.

Multiple Mating Treatment: Fifteen pairs of male and female moths (1:1 ratio) were allowed to mate throughout all scotophases during the experiment.

For nourishment, a cotton pad with a 10% honey solution was placed in a small Petri dish at the bottom of each jar. Observations were conducted using a red foil-covered 5W LED bulb in a dark environment, maintaining a 12:12 light-dark photoperiod.

2.4 Observation and Data Collection

Females were monitored from the first to the seventh day following emergence during their natural scotophase, which began at 1800 hours and ended at 0600 hours IST. Only data from the first five scotophases were included in the analysis. After egg-laying and death, copulated females were dissected to count the number of spermatophores in the bursa copulatrix, determining mating frequency (Fig. 1).

2.5 Fecundity Assessment

During the oviposition period, eggs were manually brushed from each mating jar and counted daily under a stereo-zoom binocular microscope (Fig. 2). Total fecundity was calculated by summing the daily fecundity per female.

2.6 Mating Success and Frequency

Mating success was determined by the presence of spermatophores in the bursa copulatrix, while mating frequency was gauged by counting the spermatophores. After the death of female adults, the abdomen was dissected, and from the bursa copulatrix the number of spermatophores was recorded, which provided data on mating success and frequency as described by Seth et al. [23]. The formula used was:

$$\text{Mating success \%} = \frac{\text{Number of female with one or more spermatophores}}{\text{Total number of females}}$$

2.7 Hatching/Fertility Percentage

To estimate hatching or fertility percentage, eggs were placed on a paper strip in a small Petri plate and moistened with water to prevent desiccation. Hatching was monitored twice daily, at 10 am and 5 pm. The hatching percentage was calculated using the formula:

$$Hatching\ \% = \frac{\text{Number of eggs hatched}}{\text{Total number of eggs}} \times 100$$

Statistical analysis was performed using ANOVA to evaluate the impact of mating frequency on fecundity and hatching percentage. Post hoc comparisons were conducted with Tukey's Honest Significant Difference (HSD) test, and differences were considered statistically significant at a p-value of <0.05. Treatment means were compared using the F-test and Tukey's HSD, with results expressed as mean ± SE (standard error of the mean).

3. RESULTS AND DISCUSSION

Both single-mated and multiple-mated *S. frugiperda* females exhibited 100% mating success, as evidenced by the consistent presence of spermatophores in all examined females (Fig. 1). Statistical analysis using ANOVA revealed significant differences in both fecundity and hatching percentage related-to mating frequency. The fecundity results demonstrated a substantial effect of mating frequency, with an F-value of 20.40 and a p-value < 0.05. Similarly, the hatching percentage was significantly affected, with an F-value of 16.2 and a p-value < 0.05. These results indicate that mating frequency has a marked impact on both reproductive output and egg viability in *S. frugiperda*.

The analysis of mating frequency revealed that multiple-mated females harbored between 1 and 5 spermatophores, with a mean of 2.93 ± 0.24. This is consistent with the findings of Simmons et al. [21], who reported a mean mating frequency of 3.7 for females. The presence of spermatophores in the bursa copulatrix is a useful metric for evaluating mating status and frequency, especially in the context of pest management strategies involving mating disruption and sterilization [24,25].

Egg laying was observed exclusively during the scotophase, with no activity recorded in the photophase. Females began laying eggs in the early hours of the scotophase, with the highest frequency of egg deposition occurring on the third scotophase and continuing through to the tenth (Fig. 2). The observed fecundity in multiple-mated females ranged from 803 to 2020 eggs, averaging 1468.6 ± 124.04. In contrast, single-mated females produced between 520 and 1290 eggs, with an average of 858 ± 53.36 (Fig. 3). These findings suggest that multiple mating may enhance fecundity, potentially due to the replenishment of sperm and acquisition of additional nutrients, which can contribute to increased egg production [7,8,3].

Fig. 1. Used spermatophore dissected from the bursa copulatrix of a female moth after its death, observed under a stereomicroscope

Fig. 2. Egg mass of *Spodoptera frugiperda* viewed under a stereomicroscope

Further, in lepidopteran insects, materials from spermatophores are known to contribute to egg production and somatic maintenance [5,6]**.** The increased egg production in multiple-mated females may be attributed to the nutritional benefits and hormonal effects associated with additional matings. For example, higher concentrations of vitellogenin, which is controlled by juvenile hormones, have been observed in mated females, further supporting the role of multiple matings in enhancing reproductive output [26].

Regarding hatching success, the percentage of hatched eggs from single-mated females ranged from 68% to 91%, with a mean of 78.4% ± 2.1%. For multiple-mated females, the hatching percentage varied from 81% to 97%, averaging 88.8% ± 1.5% (Fig. 4). This aligns with previous reports indicating that polyandric females, by metabolizing spermatophores more rapidly, can achieve higher offspring production and fitness compared to monogamous females [2,27]**.** Multiple matings thus offer both direct benefits, such as increased sperm availability and nutritional resources for egg production, and indirect benefits, including enhanced genetic diversity and offspring fitness [28,12].

In summary, our study highlights that increased mating frequency positively affects both fecundity and hatching success in *S. frugiperda*.

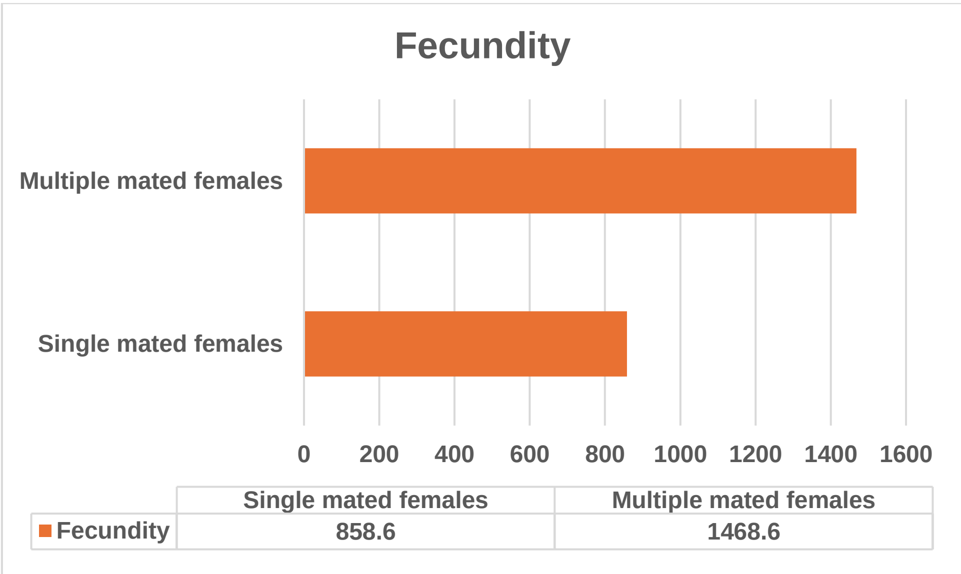

Fig. 3. Comparison of fecundity between single-mated and multiple-mated *Spodoptera frugiperda* females. The bar graph illustrates the mean fecundity (± SE) of single-mated females (n=15) and multiple-mated females (n=15). Statistical significance was determined using ANOVA followed by Tukey's HSD test ($p < 0.05$)

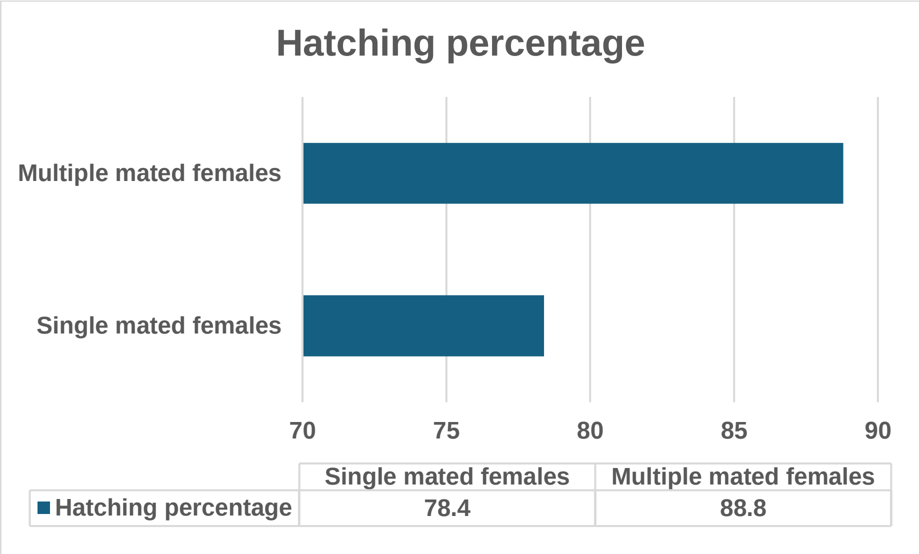

Fig. 4. Comparison of hatching percentage between single-mated and multiple-mated *S. frugiperda* females. The bar graph shows the mean hatching percentage (± SE) of eggs from single-mated females (n=15) and multiple-mated females (n=15). Statistical significance was determined using ANOVA followed by Tukey's HSD test ($p < 0.05$)

These findings have implications for pest management, suggesting that strategies which influence mating behavior could potentially enhance reproductive outcomes in this agricultural pest.

4. CONCLUSION

This study underscores the significant impact of mating frequency on the reproductive success of *S. frugiperda*. Our findings demonstrate that multiple matings enhance both fecundity and hatching success compared to single matings. Specifically, females with higher mating frequencies produced more eggs and exhibited better hatching rates, which can be attributed to the replenishment of sperm and acquisition of additional nutrients from spermatophores. This aligns with broader research on polyandry, which suggests that multiple matings offer both direct nutritional benefits and indirect genetic advantages. The observed increase in egg production and offspring viability among multiple-mated females highlights the evolutionary advantages of polyandry in enhancing reproductive output and fitness. These insights have practical implications for pest management strategies. By influencing mating behaviors, such as through mating disruption or sterilization techniques, it may be possible to manipulate reproductive outcomes in *S. frugiperda*, potentially reducing its impact on agriculture. Further research into mating strategies could provide additional avenues for effective control measures, contributing to improved pest management practices and agricultural sustainability.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declares that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during writing or editing of manuscripts.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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