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Insights into sublethal effects of *Metarhizium anisopliae* on the biotic potentials of *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) on maize

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Abstract

Background Entomopathogenic fungi are an important biological agent in integrated pest management, playing a critical role in controlling insect populations. In the present study, the sublethal effects of the entomopathogenic fungus, *Metarhizium anisopliae* (Ascomycota: Hypocreales), were investigated on the biotic potential of *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), which is a major pest of economically important crops.

Results Obtained results revealed that exposure to LC_{50} concentration of *M. anisopliae* resulted in a significantly longer larval developmental time (3.25–6.45 days) than the control group (2.42–5.49 days). Similarly, pupal duration was longer in the LC_{50} treatment (8.24 days) than in the control (6.91 days). Adult longevity was also significantly reduced in the LC_{50} (9.64 days) and LC_{30} (10.49 days) treatments compared to the control group (11.7 days). The number of eggs laid by female *S. frugiperda* exposed to LC_{50} value of *M. anisopliae* during the immature stages was significantly lower (464.79 eggs) than that in the control groups (696.93 eggs). Furthermore, all population and age-stage-specific parameters were significantly affected by the sublethal exposure to *M. anisopliae* at LC_{30} and LC_{50} values.

Conclusion These results suggest that sublethal exposure to *M. anisopliae* negatively impacts the life table parameters of *S. frugiperda*. However, the use of *M. anisopliae* at sublethal levels may have potential benefits for integrated pest management strategies seeking to reduce the use of chemicals.

Keywords *Metarhizium anisopliae*, Sublethal concentrations, Life table parameters, Fall armyworm, Reproduction, Survival

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Background

Sublethal effects of chemicals encompass biological, physiological, demographic, or behavioral changes in organisms or communities that endure exposure to a toxic substance at doses or concentrations that are either lethal or below lethal levels. When a population exposed to a toxicant survives without apparent mortality, it is termed a sublethal dose/concentration (Desneux et al. 2007). Generally, concentrations of insecticides falling below the median lethal dose/concentration (LD_{50}/LC_{50}) are categorized as sublethal. These sublethal effects can manifest as various alterations such as decreased lifespan, slower development, hindered population growth, reduced fertility, changes in reproductive capacity, shifts in gender ratios, physical abnormalities, and alterations in behaviors like feeding, searching, and egg-laying (Rimoldi et al. 2015).

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) is a highly destructive insect pest that causes extensive damage to crops in different regions of the Americas (Song et al. 2020). It has become a major threat to agricultural crops in Africa (Goergen et al. 2016), affecting a range of crops including corn, rice, sugarcane, and sorghum (Jamil et al. 2021). This pest can have multiple broods per year and is capable of traveling long distances (Abrahams et al. 2017). The immature stage of *S. frugiperda* feeds exclusively on leaves, flowers, and stalks of cultivated plants, resulting in significant economic losses (Boregas et al. 2013).

Chemical pesticides are often utilized to control *S. frugiperda* (with various types of insecticides working differently to eliminate the target pest (Casida and Durkin 2013). However, due to the adverse effects of insecticides, pest management through biological control shows significant potential (Agboyi et al. 2023). *S. frugiperda* has been effectively controlled using various entomopathogens; viruses, bacteria, fungi, protozoa, and nematodes as reported by Gómez-Valderrama et al. (2022). During severe pest outbreaks, these bioagents have been successfully utilized, as stated by Grijalba et al. (2018). Among them, entomopathogenic fungi (EPF) are noteworthy due to their wide range of hosts, pathogenicity, and capacity to manage insect pests.

Metarhizium spp., are insect-pathogenic fungi, prevalent to soil inhabitant worldwide, and have been widely studied and utilized for biological control of pests (Clifton et al. 2018)). The process of infection by *Metarhizium* spp. on insect hosts involves several stages (Aw and Hue 2017). Initially, the fungal conidia attach to the waxy cuticle of the host and germinate, producing germ tubes that differentiate into appressoria. This allows the fungus to penetrate the host via a penetration peg. The fungus employs cuticle-degrading enzymes and mechanical pressure to penetrate the insect cuticle and overcomes any stress encountered during the process (Leao et al. 2015). The fungus invades the insect hemolymph, causing insect mycosis. After the death of the host, the hyphae emerge from the cadaver and form a dense mycelial network and green spores, initiating a new round of infection (Abbas et al. 2022).

Although EPF are widely used to control pests, their potential applications are often underestimated when only considering their lethal effects. In reality, sublethal concentrations of EPF may occur in the field when the concentration of insecticides decreases gradually after the initial application, and the host is likely to be exposed to sublethal doses during that time (Abbas et al. 2022). Thus, when using *M. anisopliae* to control *S. frugiperda*, it can produce some sublethal effects. Despite numerous studies involving *Metarhizium* spp., there are limited documents about their sublethal effects on life table parameters of insects, particularly on *S. frugiperda*. The use of EPF can be a valuable and complementary approach to reduce the amount of insecticides and their drawbacks. Therefore, the present study aimed to investigate the sublethal effects of *M. anisopliae* on *S. frugiperda* using the age-stage, two-sex life table method.

Methods

Spodoptera frugiperda culture

S. frugiperda larvae were collected from a maize field located at (32° 08′ 03.1″ N 72° 41′ 23.6″ E). The larvae were provided with fresh maize leaves as food in Petri plates. The pupae were transferred to separate Petri plates. Once the adults emerged, they were placed in adult rearing cages (11 × 11 × 10 cm) and fed with a honey solution (10%). Further, maize seedlings were placed in the cages to facilitate oviposition. The insect culture was sustained under laboratory conditions of 26 ± 2 °C, 65.5 ± 5% relative humidity, and a 12:12-h light/dark cycle.

Entomopathogenic fungus

For this study, *Metarhizium anisopliae* strain Met F52 (Earth Bio-Sciences, New Haven, CT) was used which was available in the Biocontrol lab (Mubeen et al. 2022). The fungus was cultured on potato dextrose agar (PDA) plates and was incubated at 27 °C for 14 days. A spore suspension was prepared using distilled water, and a Tween® 80 solution was added at 0.1% (v/v). The spores were counted using a Neubauer chamber (Thermo Fisher Scientific, Waltham, Massachusetts, USA). The viability of the tested fungus was determined by spraying 100 µl aliquots of conidia suspension containing 10^9 conidia per ml on PDA plates. The viability of the fungus was over 90%. The suspension was adjusted to different

concentrations (1×10^3, 1×10^4, 1×10^5; 1×10^6; 1×10^7; 1×10^8, and 1×10^9 conidia ml^{-1}) and used immediately for lethal pathogenicity bioassays.

Lethal toxicity of EPF against *S. frugiperda*

For this experiment, 30 s-instar larvae of *S. frugiperda* were selected from a laboratory-cultured population and subjected to each concentration of *M. anisopliae*. Each larva was treated with approximately 4 µl from each concentration and then larvae were transferred into separate clean Petri plates containing fresh maize leaves. The mortality data were recorded after a period of 48 h. The probit analyses were performed, using POLO software, to determine the LC_{20}, LC_{30}, and LC_{50} values.

Life table study

The sublethal concentrations (LC_{20}, LC_{30}, and LC_{50}) of *M. anisopliae* were examined for their impact on the life table parameters of *S. frugiperda*. The larvae were exposed to each concentration through the topical bioassay method as described earlier. Sixty larvae were tested for each concentration with each larva considered as one replication. The treated larvae were individually placed in clean Petri plates and given fresh maize leaves daily. The developmental periods of larval instars and the pupae were recorded. After adult emergence, female and male adults were paired and placed in adult cages with maize seedlings in plastic pots and muslin cloth stripes to facilitate oviposition. The adults' longevity and fecundity rates were recorded, as well as the mortality rate of each stage.

Statistical analysis

Life table analysis

The computer program TWOSEX-MS Chart (Chi and Liu 1985; Chi 1988) was used to determine the fecundity rate, developmental time of each stage, ovipositional period, and survival rate based on an age-stage two-sex life table. The basic age-stage-specific parameters, including survival rate (s_{xj}), reproductive value (v_{xj}), life expectancy rate (e_{xj}), and population parameters such as intrinsic (r) and finite (λ) rate of increase, reproductive rate (R_0), and mean generation time (T), were also analyzed using TWOSEX-MS Chart (Chi and SU 2006). To minimize variations in results, the quick paired bootstrapping technique (Paired 1 by 1) with 100,000 replications were used to estimate the mean and standard error of the population (Efron and Tibshirani 1993) with the TWOSEX-MS Chart program.

Results

The LC_{50}, LC_{30}, and LC_{20} values were obtained from the mortality concentration–response and were found as 3.6×10^7, 5.4×10^4, and 1.04×10^3 conidia ml^{-1}, respectively, based on the lethal toxicity for seven serial dilutions. These sublethal concentrations were utilized to investigate their effects on life table parameters of *S. frugiperda*. Table 1 provides the developmental time of each larval instar of *S. frugiperda*, which was significantly ($p<0.05$) different across treatments. In general, larvae developed faster in the control group (2.42–5.49 days) than when LC_{50} value was applied, which prolonged the period (3.25–6.45 days). Similarly, the pupal duration was prolonged after applying LC_{50} (8.24 days) than control (6.91 d). The adult longevity was shorter in LC_{50} (9.64

Table 1 Development period (days) of *Spodoptera furgiperda* after exposure to sublethal concentration of *Metarhizium anisopliae*

Stages	*N*	Control	*n*	LC_{20}	*n*	LC_{30}	*n*	LC_{50}
Egg	60	2.82 ± 0.05ab	60	2.85 ± 0.05a	60	2.65 ± 0.07b	60	2.48 ± 0.07c
L1	60	2.42 ± 0.07b	60	2.42 ± 0.07b	60	3.08 ± 0.12a	60	3.25 ± 0.09a
L2	60	2.80 ± 0.78bc	60	2.75 ± 0.08c	60	3.40 ± 0.10b	60	3.65 ± 0.07a
L3	60	3.48 ± 0.11c	58	3.81 ± 0.13ab	59	3.76 ± 0.10b	56	4.16 ± 0.08a
L4	59	4.10 ± 0.16b	55	4.44 ± 0.16ab	54	4.26 ± 0.09b	45	4.64 ± 0.09a
L5	58	4.48 ± 0.14c	53	4.98 ± 0.18b	49	5.27 ± 0.17ab	33	5.52 ± 0.14a
L6	57	5.49 ± 0.13c	51	5.98 ± 0.16b	47	6.06 ± 0.13b	33	6.45 ± 0.12a
Pupa	57	6.91 ± 0.18c	49	7.59 ± 0.22b	47	8.02 ± 0.13ab	33	8.24 ± 0.12a
Adult	57	11.7 ± 0.24a	49	11.7 ± 0.33ab	47	10.4 ± 0.25c	33	9.64 ± 0.23d
Male	29	44.4 ± 0.90b	19	46.3 ± 0.95ab	20	45.1 ± 0.73ab	14	46.7 ± 0.66a
Female	28	44.0 ± 0.77c	30	46.0 ± 0.1.06bc	27	48.0 ± 0.68ab	19	48.6 ± 0.67a
Nf/N		0.46 ± 0.06ab		0.50 ± 0.06a		0.45 ± 0.06ab		0.31 ± 0.06b

SE was estimated by bootstrapping (100,000 replications), L1-L6 indicate the larval instar, n = shows the number of individuals, $LC_{20}=1.04\times10^3$, $LC_{30}=5.4\times10^4$ and $LC_{50}=3.6\times10^7$, means sharing similar letters are not significantly different, determined using the paired bootstrap test ($p<0.05$), and L1-L6 shows the larval instars

days), followed by LC_{30} (10.49 d), and LC_{20} (11.73 days), compared to control (11.7 d) (Table 1).

APOP and TPOP periods were longer in LC_{30} (3.07 and 39.8 days, respectively) and LC_{50} treatments (2.79 and 41.4 days, respectively). The ovipositional period of the female was shortened (2.9 days) when LC_{50} and LC_{30} values were applied, compared to the control group (3.54 days). The females laid the least number of eggs (464.79 eggs), when LC_{50} value of *M. anisopliae* was applied than those in control (696.93 eggs). The r (0.114 d^{-1}) and R_0 (147.1 offspring) values of *S. frugiperda* reduced when LC_{50} of *M. anisopliae* was applied than of the control group ($r=0.156$ d^{-1} and $R_0=325.2$ offspring). On the other hand, the λ value increased to (1.120 d^{-1}) in the LC_{50} treatment than control ($\lambda=0.169$ d^{-1}). The generation time lasted longer (43.7 days) when LC_{50} was applied than in the control (36.9 d) (Table 2).

Figure 1 illustrates the s_{xj} (age-specific survival rate) value of *S. frugiperda* after exposure to *M. anisopliae*. In the control group, male and female adults emerged

Table 2 Life table and reproductive parameters (means ± SE) of *Spodoptera frugiperda* after exposure to sublethal concentration of *Metarhizium anisopliae*

Parameters	Control	LC_{20}	LC_{30}	LC_{50}
APOP	2.75 ± 0.13ab	2.67 ± 0.13b	3.07 ± 0.11a	2.79 ± 0.12ab
TPOP	34.6 ± 0.73c	36.9 ± 0.88b	39.8 ± 0.55a	41.1 ± 0.66a
Oviposition days	3.54 ± 0.10a	3.13 ± 0.08b	2.96 ± 0.04c	2.95 ± 0.05c
Fecundity	696.9 ± 15.2a	611.9 ± 20.6b	598.5 ± 18.3b	464.7 ± 14.6c
R_0 (offspring)	325.2 ± 45.2a	305.9 ± 40.9a	269.33 ± 38.9a	147.1 ± 28.2b
r (d^{-1})	0.156 ± 0.005a	0.146 ± 0.004a	0.131 ± 0.004b	0.114 ± 0.004c
λ (d^{-1})	0.16 ± 0.006a	1.15 ± 0.005a	1.14 ± 0.004b	1.12 ± 0.005c
T (d)	36.9 ± 0.77b	39.0 ± 0.89b	42.6 ± 0.61a	43.7 ± 0.69a

Means with similar letters are not significantly different ($p<0.05$), $LC_{20}=1.04\times10^3$, $LC_{30}=5.4\times10^4$ and $LC_{50}=3.6\times10^7$, APOP = adult pre-oviposition periods, TPOP = total pre-oviposition periods, T = mean generation time, r = intrinsic rate of increase, λ = finite rate of increase, R_0 = net reproductive rate

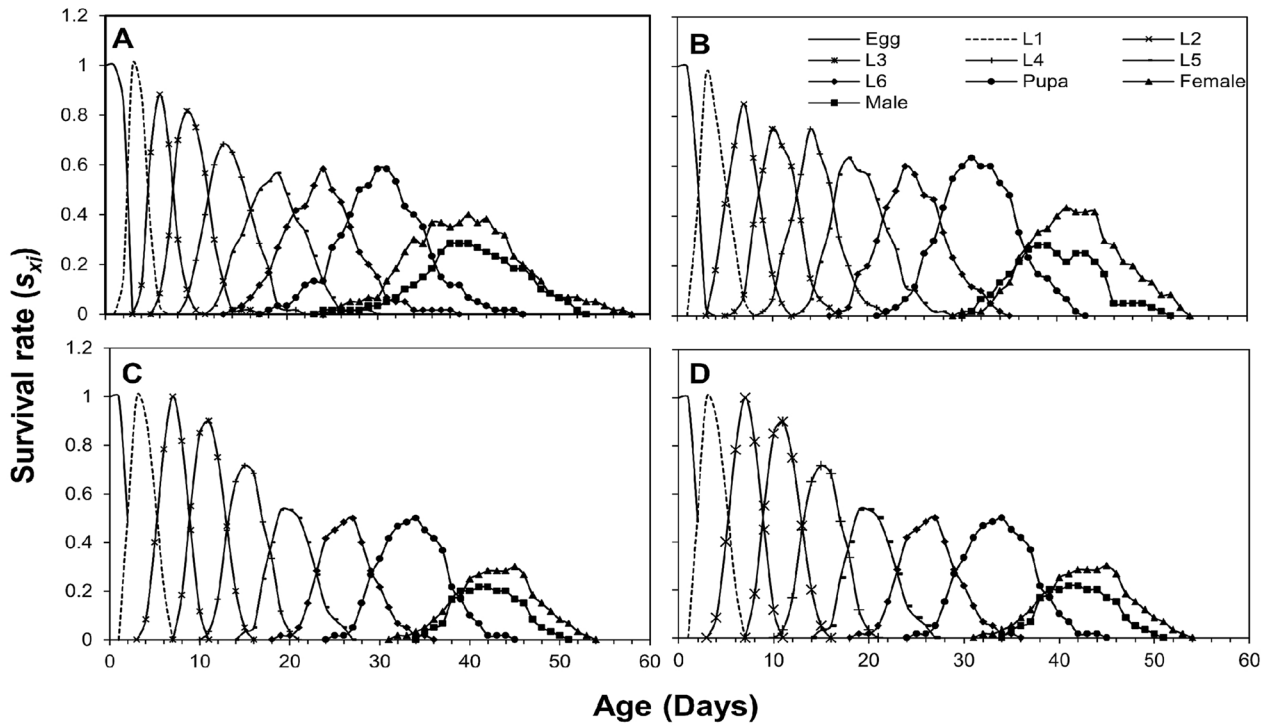

Fig. 1 Age-stage-specific survival rate (s_{xj}) of *Spodoptera frugiperda* after exposure to sublethal concentration of *Metarhizium anisopliae*. **A**: LC_{20}, **B**: LC_{30}, **C**: LC_{50}, and **D**: Control

at 24th and 25th day, respectively. In the LC_{50} treatment group, males and females emerged at 35th and 32nd day, respectively (Fig. 1). The e_{xj} curve indicated that the life expectancy of *S. frugiperda* treated with all sublethal concentrations of *M. anisopliae* was lower than the control group. At age zero (e_{01}), e_{xj} of *S. frugiperda* was 42.9 days in the control group, 33.6 days in LC_{50}, 40.4 days in LC_{30}, and 41.2 days in LC_{20} (Fig. 2). The v_{xj} showed the future population growth of individuals of age *x* and stage *j*. It showed that the highest reproductive value for females was observed in the control group at age 31st, whereas a low peak was recorded on 40th day in the LC_{50} treatment. In LC_{30} and LC_{20} treatments, high peaks were observed on 39th and 28th days, respectively (Fig. 3). The fecundity rate of *S. frugiperda* female appeared later in the treatment groups than in the control. The maternity rate of *S. frugiperda* peaked at later ages in the treatment groups as well (Fig. 4).

Discussion

Metarhizium anisopliae is a well-known entomopathogenic biological control agent that has been used to control various insect pests, including *S. frugiperda* (Mubeen et al. 2022). Although previous studies have determined the lethal effects of *M. anisopliae* on *S. frugiperda* (Mubeen et al. 2022), the sublethal effects of this fungus on the life table parameters of *S. frugiperda* remain unclear. In the present study, *S. frugiperda* were exposed to sublethal concentrations of *M. anisopliae* spores and monitored their survival, development, and reproductive parameters. The results showed that exposure to *M. anisopliae* at LC_{50} and LC_{30} had significant sublethal effects on the developmental period of *S. frugiperda*, leading to a longer period and decreased fecundity in female insects as compared to the control group. The prolongation in larval and pupal periods may occur because the energy that would typically support larval growth is instead directed toward detoxifying the toxin compounds generated by entomopathogenic fungi. This aligns with the study of Afriyanita et al. (2019), who highlighted that these toxic compounds can hinder larval development. Instead of being used into growth and development, the energy derived from food is redirected toward the detoxification process to counteract the effects of the toxic substances.

The present study's findings align with previous research that has shown that the sublethal effects of *M. anisopliae* on the developmental period of *S. frugiperda* and other insect pests. For instance, Mwamburi (2021) reported that treatment with *M. anisopliae* resulted in a prolonged developmental period and reduced larval weight in *S. frugiperda*. Similarly, Jarrahi and Safavi (2016) found that sublethal concentrations of *M. anisopliae* extended the developmental

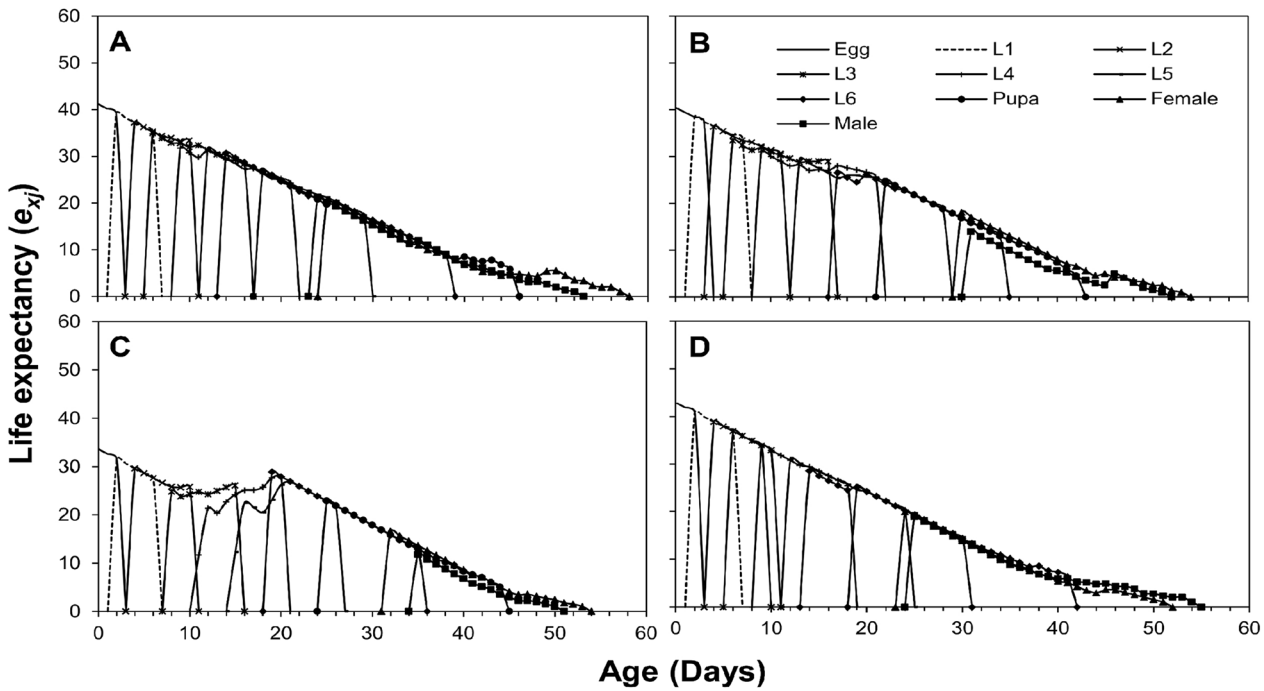

Fig. 2 Age-stage-specific life expectancy (e_{xj}) of *Spodoptera frugiperda* after exposure to sublethal concentration of *Metarhizium anisopliae*. **A**: LC_{20}, **B**: LC_{30}, **C**: LC_{50}, and **D**: Control

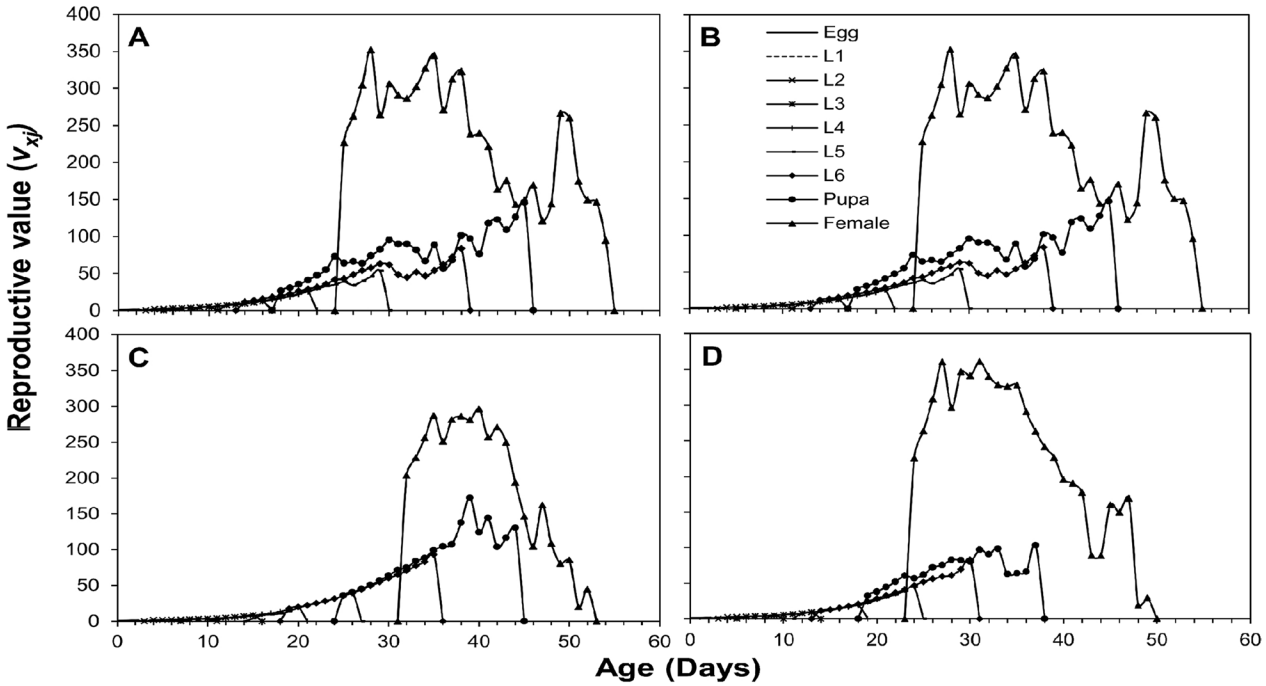

Fig. 3 Age-stage-specific reproductive value (v_{xj}) of *Spodoptera frugiperda* after exposure to sublethal concentration of *Metarhizium anisopliae*. **A**: LC_{20}, **B**: LC_{30}, **C**: LC_{50}, and **D**: Control

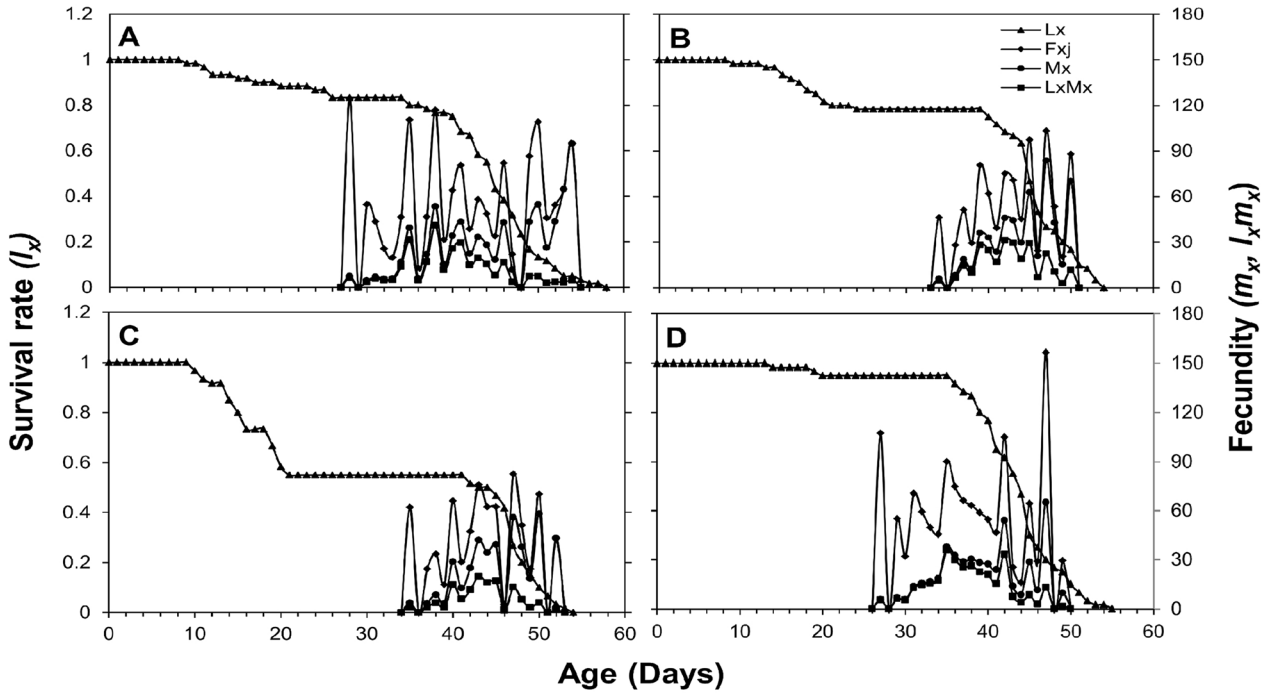

Fig. 4 Age-stage-specific survival rate (l_x), age-stage-specific fecundity (f_{xj}), age-specific fecundity (m_x) and age-specific maternity (l_xm_x) of *Spodoptera frugiperda* after exposure to sublethal concentration of *Metarhizium anisopliae*. **A**: LC_{20}, **B**: LC_{30}, **C**: LC_{50}, and **D**: Control

phase of immature stages of the cotton bollworm, *Helicoverpa armigera* (Hb.). These findings suggest that *M. anisopliae* negatively affects insect growth and development, possibly by reducing feeding and growth rates caused by the infection (Idrees et al. 2021). However, it is worth noting that efficacy of *M. anisopliae* can vary depending on the timing and frequency of applications (Sánchez-Peña et al. 2011) and environmental factors such as temperature and humidity (Kamga et al. 2022). *M. anisopliae* employs various mechanisms to infect and kill insect pests, including direct infection, production of insecticidal toxins, and induction of immune responses in the host insect (Aw and Hue 2017). In addition, *M. anisopliae* produces a range of secondary metabolites that are toxic to insect pests, such as destruxins, which disrupt insect cell membranes and cause cell death (Sbaraini et al. 2016).

The present study demonstrated that the exposure of *S. frugiperda* to *M. anisopliae* resulted in a significant reduction in the egg-laying capacity of female insects, especially at LC_{50} and LC_{30} values. This finding is consistent with those reported by Zafar et al. (2020) on *Plutella xylostella*. Reduced reproductive fitness may be attributed to a variety of factors, including changes in hormone levels, reduced nutrient uptake, and the diversion of resources to immune responses (Schwenke et al. 2016). Additionally, increased conidial concentration may also contribute to this effect by redirecting host resources such as energy, to the pathogen (Roy et al. 2006). The findings are also supported by previous studies that reported sublethal effects of EPF on the fecundity rate of insect pests (Pelizza et al. 2013).

Examination of life table parameters is crucial in identifying the sublethal impacts of EPF on insect survival, development, and reproduction. The results indicated significant changes in the life table parameters r, R_0, and T of *S. frugiperda*, with lower values of r and R_0 observed in the LC_{30} and LC_{50} groups than the control. These results are similar to those obtained by De Souza et al. (2020) on *H. armigera*. Additionally, the present study showed that the sublethal concentrations of LC_{30} and LC_{50} had notable effects on s_{xj}, e_{xj}, and v_{xj} values. The mortality rate of insects was high in the treated groups, with high mortality rates observed in the latest developmental stages. The survival rate can serve as an indicator of insect population growth following exposure to fungal treatment (Huang and Chi 2012). Our findings revealed the negative impact of *M. anisopliae* on *S. frugiperda* as evidenced by the lowest s_{xj} of each age stage relative to the control and the linear downward trend of l_x of the population. Moreover, the reproductive values of female in the LC_{30} and LC_{50} groups decreased than the control, as indicated by the v_{xj} and e_{xj} values. These results are consistent with those of Xia et al. (2023) who investigated the effects of *B. bassiana* against various insects.

The present study highlighted also the negative impact of *M. anisopliae* on the growth and survival of *S. frugiperda*, which is crucial information for developing effective pest management strategies (Zhang et al. 2015). It is important to note, however, that the efficacy of EPF in pest management program depends on their virulence toward target pests and their safety for non-target organisms. Therefore, it is important to estimate the impact of sublethal concentrations of EPF on natural enemies to ensure their reliable and applicable outcomes. Additionally, the use of chemical insecticides in the same environment may reduce the effectiveness of EPF by negatively affecting their conidial survival. Therefore, it is crucial to determine the compatibility of tested EPF with chemical insecticides used in an IPM program).

Conclusion

The findings revealed noteworthy alterations in all population and age-stage-specific parameters as a result of sublethal exposure to *M. anisopliae* at LC_{30} and LC_{50} values. This underscores the considerable influence of the fungal treatment on the survival, development, and reproductive dynamics of *S. frugiperda* populations. The outcomes of this study emphasize the significance of considering sublethal effects when assessing the impact of *M. anisopliae* as a potential biological control agent against *S. frugiperda*, shedding light on the broader implications of its employment in pest management strategies. Further investigations are needed to better understand the sublethal effects of *M. anisopliae* on other insect pests and to develop more effective and sustainable pest control approaches.

Abbreviations

EPF	Entomopathogenic fungi
s_{xj}	Survival rate
v_{xj}	Reproductive value
e_{xj}	Life expectancy rate
r	Intrinsic rate of increase
λ	Finite rate of increase
R_0	Reproductive rate
T	Mean generation time

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Author contributions

MIU and MA contributed to conceptualization; MIU provided methodology; MA, SSA, SMS, and MR provided software; MIU, US, MAR, and MM performed validation; MA, SSA, OMA, MM, SMS, and MR carried out formal analysis; MIU performed investigation and supervision; SK, LAA, SSA, OMA, MM, and SMS provided resources; AM and MQ performed data curation; MQ and MA performed writing—original draft preparation; MAR, SSA, SMS, OMA, MM, and HMA performed writing—review and editing; SK performed visualization; MIU and MAR performed project administration; LAA, SSA, OMA, and SMS

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Availability of data and materials
All data generated or analyzed in this work are available in the published manuscript.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
This study does not contain any individual person's data.

Competing interests
The authors declare not to have any competing interests regarding the publication of this work.

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