SURVIVAL FITNESS OF *SPODOPTERA FRUGIPERDA* CONSEQUENT TO CANNIBALISM BEHAVIOUR

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Abstract. Cannibalism is a common phenomenon in insects including fall army worm, *Spodoptera frugiperda*. The purpose of the present investigation was to understand the fitness benefits of cannibalism in *S. frugiperda*. The investigation was carried out at the University of Agricultural Sciences, Dharwad (Karnataka-India) during 2020-21. Cannibalism was studied at different larval stages of *Spodoptera frugiperda*. Though no cannibalism was observed among 1st instar larvae up to 72 h of interaction, as high as 84% cannibalism was recorded in the case of 2nd instar larvae. The rate of cannibalism was relatively high when different instar larvae interacted with each other with maximum cannibalism (90%) evidenced in the case of 2nd instar v/s 3rd and 4th instar larval treatments after 72 h of interaction as compared to late larval instars indicating that early or mid-aged larvae were more succumbed to cannibalism. The substantial cannibalism led to reduced pupation and adult emergence along with malformation of pupae and adults.
Keywords: *cannibalism, interaction, Spodoptera frugiperda*

Introduction

Maize or corn (*Zea mays* L.) is an important annual cereal crop of the world belonging to family Poaceae. Zea is an ancient Greek word which means "sustaining life" and Mays is a word from Taino language meaning "life giver" (Kumar and Jhariya, 2013). It is considered as a staple food crop in many parts of the world. It is the third leading crop of the world after rice and wheat (Sandhu et al., 2007). Due to its highest yield potential among the cereals, it is known globally as the "Queen of cereals." In India, the major maize growing states are Uttar Pradesh, Bihar, Rajasthan, Madhya Pradesh, Punjab, Haryana, Maharashtra, Andhra Pradesh, Himachal Pradesh, West Bengal, Karnataka, and Jammu and Kashmir, jointly accounting for over 95% of the national maize production (Milind and Isha, 2013).

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) is native to the Americas and it is a key pest of maize (*Zea mays* L.). The fall armyworm has been reported for the first time in 2016 in Africa, in Nigeria, causing significant damages to maize. This pest has been detected for the first time in the Indian subcontinent in mid-May 2018 in maize fields in Southern parts of Karnataka. Being a polyphagous pest, FAW is known to cause major damage to economically important cultivated grasses such as rice, sorghum, maize and sugarcane as well as cabbage, beet, peanut, soybean, alfalfa, onion, cotton, pasture grasses, millet, tomato and potato (Ankush et al., 2019).

Cannibalism is the killing and consumption of all or part of conspecific individuals which is a ubiquitous phenomenon with most important ecological and evolutionary implications in almost all major vertebrate and invertebrate groups. Cannibalism is a

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frequent behavior in a wide array of animal taxa, often accounting for substantial mortality that may influence population dynamics and community structure. Cannibalism has been widely documented in larval lepidoptera, although there is considerable variation in the frequency of cannibalistic behavior in closely related species. In many cases however, the selective advantages associated with cannibalism remain to be elucidated.

Cannibalism may confer direct (nutritional) fitness benefits in the form of increased survival, developmental rate and fecundity or it may provide indirect benefits by removing potential competitors and intraspecific predators. A third possible benefit associated with cannibalism may be a reduction in the risk of predation and/or parasitism via decreases in local population density. On the other side, cannibalism is not conducive to the growth and development of *S. frugiperda* (Tang et al., 2022). Cannibalism was characterized here as one larvae feeding on the other and resulting mortality. The cannibalism of the older larvae to the younger larvae increased with the increase of the density of the younger larvae (Mbuji et al., 2022). Larvae shows cannibalistic behavior as a function of temperature and amount of food (Machado et al., 2021). Since, it is very difficult to distinguish different degrees of larval cannibalism including tentative attack (bite), counterattack, chase, wrap and eating in case of *H. armigera* (Li et al., 2006), we attempted to characterize the behavioral aspects of cannibalism in *S. frugiperda.*

In case of *S. frugiperda* also cannibalism behavior is very prominent and probably the reason for low population densities irrespective of number of eggs laid on individual maize plants. Further, this behavior might also affect the population of other species appearing simultaneously on the crop. The main objective of this study to determine the cannibalism interaction among different larval instars of *S. frugiperda* and resultant relative influence on pupation and adult emergence in surviving individuals of progeny generation.

Materials and methods

Insect culture

Egg masses of fall armyworm were collected from the corn field and reared to get nucleus culture. The caterpillars were reared up to adult stage. Further, a pair of freshly emerged adult moths were released into wooden cage (36 × 36 × 36 cm size) for oviposition where in provision were made with 10% honey solution as food and fresh tender maize leaves were provided inside the cage for oviposition. The cut end of leaves was covered with a wet cotton wad for maintaining turgidity and freshness.

Freshly laid eggs were kept in rearing boxes provided with wet blotting paper at the bottom to protect the eggs from desiccation. After two days when eggs turn to black purple color, they were provided with fresh maize leaves as food for neonate larvae. The neonate larvae were released on leaves with the help of soft hair brush and kept in a rearing box whose cap were covered with muslin cloth in order to facilitate aeration. The food was changed after every 24 h.

Interaction studies

Investigations were made under laboratory conditions in the Department of Agricultural Entomology, University of Agricultural Sciences, Dharwad during 2020-21. Fifteen treatments with five replications comprising interaction among the individual instar-wise larval treatments (treatments 1 to 6) and interaction between

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different instars of *S. frugiperda* larvae (treatments 7 to 15) were planned. The laboratory reared larvae were starved for 1 h before the initiation of the experiment. Five larvae (stadium according to *Table 1*) of each instar were placed into transparent Petri plates containing a wet blotting paper to maintain the moisture. Each Petri plate was considered as one replicate, with 5 replicates in a completely randomized design. Fresh maize leaves cleaned with 92.8% ethanol were provided to each petri plate as larval food and replaced on daily basis.

Counts on larval survival were performed at 12, 24, 48 and 72 h after release of larvae in each treatment and percent cannibalism was worked out. At the end of the larval period in each of the treatment the total cannibalism was noted. Out of survived larvae, percent pupation and adult emergence along with deformation were recorded treatment wise. Behavioral interactions among different larval instars in respect of cannibalism like biting, partial feeding, complete feeding were also noted.

Statistical analysis

After the square arcsine transformation of data, the cannibalism rates of the same instar larvae with same instar larvae and different instar larvae, and impact of cannibalism on pupation and adult emergence were subjected to Analysis of Variance (ANOVA). When the ANOVA results were significant, multiple comparisons of means were performed with Duncan's Multiple Range Test. The results were presented as means ± standard errors (SEs).

Results

Cannibalism among same larval instars

No cannibalism was observed among first instar larvae up to 72 h of interaction (*Table 1*). But high rate of cannibalism was witnessed among second instar larvae at all intervals leading to a total of 84% cannibalism. As the instar advanced the cannibalism rate decreased (72% in 3rd instar larvae to 32% in 6th instar larvae after 72 h).

Table 1. *Cannibalism among same instars of Spodoptera frugiperda*

Tr. no.	Treatments	Cannibalism (%) at				
		12 h	24 h	48 h	72 h	Total
T1	1st instar larvae	0.00 ± 0.00^{c}	0.00 ± 0.00^{c}	0.00 ± 0.00^{c}	0.00 ± 0.00^{c}	0.00 ± 0.00^{e}
T2	2nd instar larvae	22.00 ± 13.04^{a}	22.00 ± 13.04^{a}	22.00 ± 8.36^{a}	18.00 ± 10.95^{a}	84.00 ± 5.48^{a}
T3	3rd instar larvae	20.00 ± 7.07^{a}	12.00 ± 4.47^{b}	22.00 ± 4.47^{a}	18.00 ± 8.36^{a}	72.00 ± 2.73^{b}
T4	4th instar larvae	18.00 ± 4.47^{ab}	14.00 ± 5.47^{ab}	6.00 ± 5.47^{bc}	10.00 ± 0.61^{ab}	48.00 ± 2.73^{c}
T5	5th instar larvae	12.00 ± 8.36^{ab}	8.00 ± 4.47^{bc}	12.00 ± 7.07^{b}	2.00 ± 4.47^{bc}	34.00 ± 2.23^{d}
T6	6th instar larvae	8.00 ± 8.36^{bc}	12.00 ± 4.47^{b}	8.00 ± 4.47^{b}	4.00 ± 5.47^{bc}	32.00 ± 2.73^{d}

At pupation time, the total cannibalism was maximum (92%) in 2nd instars followed by third, fourth and fifth instars with a cannibalism of 76% leading to proportionate reduced pupation and adult emergence in those treatments. The other treatments with relatively higher pupation and formation of adults, particularly the treatments with late instar larvae resulted in maximum malformation of pupae and deformed adults (*Table 2*).

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Table 2. *Impact of cannibalism on pupation and adult emergence among same instars*

Larval instars	Percent cannibalism at pupation	Percent pupation		Percent adult emergence	
		Total	Malformed	Total	Malformed
1st instar	60.00 ± 2.51^{c}	40.00 ± 1.67^{b}	12.00 ± 0.50^{a}	24.00 ± 1.00^{b}	8.00 ± 0.33^{a}
2nd instar	92.00 ± 7.83^{a}	8.00 ± 0.68^{d}	4.00 ± 0.34^{c}	4.00 ± 0.34^{e}	0.00 ± 0.00^{c}
3rd instar	76.00 ± 3.60^{b}	24.00 ± 0.14^{c}	8.00 ± 0.38^{b}	16.00 ± 0.76^{d}	4.00 ± 0.19^{b}
4th instar	76.00 ± 6.15^{b}	24.00 ± 0.94^{c}	4.00 ± 0.32^{c}	20.00 ± 1.62^{c}	4.00 ± 0.32^{b}
5th instar	76.00 ± 4.78^{b}	24.00 ± 1.51^{c}	8.00 ± 0.50^{b}	16.00 ± 1.01^{d}	4.00 ± 0.25^{b}
6th instar	52.00 ± 3.64^{d}	48.00 ± 0.36^{a}	8.00 ± 0.56^{b}	40.00 ± 2.80^{a}	8.00 ± 0.56^{a}

Cannibalism interaction among different larval instars of Spodoptera frugiperda

When the first instar larvae were allowed to interact with third and fourth instar larvae, the total cannibalism was to the tune of 88 and 80%, respectively after 72 h of interaction. While, maximum of 90% cannibalism was recorded when 2nd instar larvae interacted with 3rd or 4th instar larvae indicating that early or mid-aged larvae are more succumbed to cannibalism (*Table 3*). The rate of cannibalism was relatively low when 3rd instar larvae were exposed to 4th and 5th larval instars (60 and 50%, respectively after 72 h). Similarly, as low as 44 and 42% cannibalism was recorded in case of 4th instar larvae v/s 5th and 6th instar larvae, respectively after 72 h of interaction.

Table 3. *Cannibalism Interaction among different larval instars of Spodoptera frugiperda*

Treatment details		Percent cannibalism				
		12 h	24 h	48 h	72 h	Total
1st instar v/s	3rd instar	18.00±8.36^{c} (14.00+4.00)	37.00±8.36^{a} (16.00+11.00)	28.00±8.36^{a} (18.00+11.00)	12.00±4.47^{a} (0.00+12.00)	88.00±8.48
	4th instar	20.00±10.00^{c} (16.00+4.00)	28.00±8.36^{b} (16.00+12.00)	20.00±7.07^{b} (16.00+4.00)	12.00±4.47^{a} (2.00+10.00)	80.00±6.53
2nd instar v/s	3rd instar	30.00±12.24^{b} (22.00+8.00)	26.00±5.47^{b} (16.00+10.00)	28.00±16.43^{a} (12.00+16.00)	6.00±5.47^{c} (0.00+6.00)	90.00±11.12
	4th instar	44.00±15.16^{a} (34.00+10.00)	36.00±15.16^{a} (16.00+20.00)	8.00±4.47^{d} (0.00+8.00)	2.00±4.47^{d} (0.00+2.00)	90.00±20.61
3rd instar v/s	4th instar	28.00±10.95^{b} (18.00+10.00)	18.00±4.47^{c} (12.00+6.00)	8.00±8.36^{d} (4.00+4.00)	6.00±8.94^{c} (2.00+4.00)	60.00±10.13
	5th instar	18.00±8.36^{c} (10.00+8.00)	8.00±4.47^{e} (6.00+2.00)	12.00±4.47^{c} (6.00+6.00)	12.00±8.36^{a} (6.00+6.00)	50.00±4.12
4th instar v/s	5th instar	12.00±4.47^{d} (8.00+4.00)	10.00±7.07^{e} (4.00+6.00)	12.00±8.36^{c} (6.00+6.00)	10.00±7.07^{b} (6.00+4.00)	44.00±1.154
	6th instar	6.00±5.47^{e} (6.00+0.00)	14.00±5.47^{d} (8.00+6.00)	12.00±8.36^{c} (6.00+6.00)	10.00±4.47^{b} (2.00+8.00)	42.00±3.41

Impact of cannibalism on pupation and adult emergence among different instars

In the interaction studies, at pupation time, the total cannibalism was maximum (92%) in 2nd instar interacted with 3rd and 4th instar alone and 1st instar interacted with 4th instar larvae leading to reduced pupation and adult emergence in those treatments.

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The other treatments with relatively higher pupation and formation of adults, particularly the treatments with late instar larvae resulted in maximum malformation of pupae and deformed adults (*Table 4*).

Table 4. *Impact of cannibalism on pupation and adult emergence among different instars*

Treatment details	Percent cannibalism at pupation	Percent pupation		Percent adult emergence	
		Total	Malformed	Total	Deformed
1st instar v/s 3rd instar larvae	84.00 ± 4.07^{b}	16.00 ± 0.78^{c}	0.00 ± 0.00^{d}	16.00 ± 0.78^{c}	4.00 ± 0.19^{b}
1st instar v/s 4th instar larvae	92.00 ± 6.67^{a}	8.00 ± 0.58^{d}	0.00 ± 0.00^{d}	8.00 ± 0.58^{d}	4.00 ± 0.29^{b}
2nd instar v/s 3rd instar larvae	92.00 ± 4.32^{a}	8.00 ± 0.38^{d}	0.00 ± 0.00^{d}	8.00 ± 0.38^{d}	0.00 ± 0.00^{c}
2nd instar v/s 4th instar larvae	92.00 ± 7.19^{a}	8.00 ± 0.62^{d}	4.00 ± 0.31^{c}	4.00 ± 0.31^{e}	0.00 ± 0.00^{c}
3rd instar v/s 4th instar larvae	56.00 ± 2.34d^{d}	44.00 ± 1.84^{a}	12.00 ± 0.50^{a}	32.0 ± 1.34^{a}	4.00 ± 0.17^{b}
3rd instar v/s 5th instar larvae	76.00 ± 6.47^{c}	24.00 ± 2.04^{b}	8.00 ± 0.68^{b}	16.0 ± 1.36^{c}	0.00 ± 0.00^{c}
4th instar v/s 5th instar larvae	76.00 ± 3.60^{c}	24.00 ± 1.14^{b}	4.00 ± 0.19^{c}	20.0 ± 0.95^{b}	4.00 ± 0.19^{b}
4th instar v/s 6th instar larvae	56.00 ± 4.53d^{d}	44.00 ± 3.56^{a}	12.00 ± 0.97^{a}	32.0 ± 2.59^{a}	8.00 ± 0.65^{a}

Discussion

Cannibalism is ubiquitous in the animal kingdom and widely occurs in many species of lepidopterous larvae, such as in the fall armyworm, *Spodoptera frugiperda*, the corn earworm, *Helicoverpa zea* and the beet armyworm, *S. exigua* (Hübner) (Stinner et al., 1977; Chapman et al., 2000; Horner and Dively, 2003; Williams and Hernández, 2006; Elvira et al., 2010). The results of present study conclude that cannibalism is also a biological phenomenon from the beginning of second-instars to fifth-instar larvae in *S. frugiperda*.

The results of the studies indicated that, cannibalism is not an artifact of laboratory condition or limited to non-availability of food. Present investigation on cannibalism in *S. frugiperda* in the presence of food under laboratory revealed no cannibalism among 1st instar larvae probably due to lack of well-developed mouthparts as reported by Chapman et al. (1999a, b). Relatively low cannibalism was noticed among the same instars as compared to interaction between the different instars. It is observed that since the larval age was same, no competition between the individuals for food was witnessed. Similarly, Reynolds (1980) also opined that the cannibalism between same instar, inter molting larvae of *S. frugiperda* would be highly unlikely but however, under more confined conditions, such as in a petri plate, cannibalism might be more frequent between same-instar larvae. The maximum cannibalism observed in case of 2nd instar v/s 3rd and 4th instar larval treatments can be attributed to more activeness and vigorous nature of 4th instar and 3rd instar larvae compared to other instars (Dial and Alder, 1990). The first instar larvae owing to their under developed mouth parts have experienced less cannibalism instead they fed on the tender corn leaves provided as a source of food. Second instar larvae exhibited maximum cannibalism with 3rd and 4th instar larvae. We hypotheses that as the larvae grew up to second instar, there was a gradual development of mandibles leading to maximum biting and partial feeding among conspecific instars. In early instar the partial feeding and biting has resulted in to the complete mortality of the affected larvae as against recovery in case of 4th and 5th instar larvae following biting and partial feeding. However, in the later instars as they are physical strong and aggressive, the

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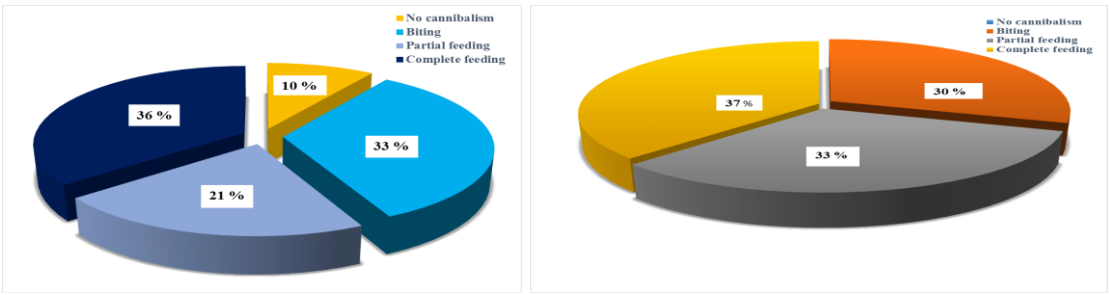
phenomenon of partial feeding and biting was not so frequent instead complete feeding leading to death of the larvae. The study concluded that in 2nd instar larvae, the major behavior of cannibalism is biting and partial feeding whereas in case of later instars it is mainly the complete feeding as the later instars defend themselves to survive. The second hypothesis is that the larvae attaining the pre-pupal stage are more succumbed to cannibalism by the developing late instars larvae. The inactiveness exhibited by the pre-pupal larvae has benefitted the other developing larvae leading to more cannibalism in the pre-pupal stage.

Kakimoto et al. (2003) reported that cannibalistic frequency between same-instar larvae was lower than that between larvae of different ages. Cases in which older instar larvae were cannibalized by younger instar larvae were rare and all cases were observed in combats between larvae of adjacent instars. In the present study, the highest mortality was observed in the third and fourth instars interacted with second instar on natural diets comparing with those in fifth and sixth instars interacted with fourth instar, suggesting cannibalistic behavior occurred frequently among subsequent aged larvae of middle instars

The miniature adults emerged from the malformed pupae due to cannibalism may lead to lower fecundity and hence, reduced population. Formation of malformed pupae due to cannibalism may be attributed for failure in ecdysis or starvation. Kakimoto et al. (2003) also noticed reduced percent pupation in case of *Helicoverpa armigera* under suitable food conditions. Laboratory studies of the adaptive benefits of cannibalism in larval *S. frugiperda* indicated that cannibals suffer heavy costs. Cannibals have significantly lower survival, lower body weight and hence reduced female fecundity (Lynch, 1984).

Early instar larvae were completely eaten by late instar larvae. However, either the early instar larvae or the late instar larvae exhibited cannibalism through biting and partial feeding behavior among themselves. Early instar larvae fed on the hemolymph of the injured late instar larvae as observed in case of *H. armigera* by Dial and Alder (1990) (*Figs. 1* and *2*).

Some interesting findings were achieved during the process of these experiments, such as the larvae with high frequency of cannibalism have less pupation and adult emergence. The early instar larvae preferred the cannibalized larval hemolymph over the natural food. The biting and partial feeding are the common behavior of cannibalism in case of 2nd instar larvae compared to complete feeding in later instars. These results suggests that cannibalism is a behavior of *S. frugiperda* larvae, which may have been evolved to eliminate potential intraspecific competitors, and thereby to escape from unsuitable conditions.



Among same instar larvae **Among different instar larvae**

Figure 1. *Cannibalism behavior of Spodoptera frugiperda*

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Larvae feeding on hemolymph **5th instar larva feeding on 2nd instar larva**

Figure 2. *Cannibalism behavior of Spodoptera frugiperda*

Conclusion

Laboratory investigations clearly indicated frequent cannibalism in *S. frugiperda* even in the presence of its natural food. But however, no cannibalism was observed among 1st instar larvae up to 72 h in comparison to a maximum cannibalism of 84% in case of 2nd instar larvae. The rate of cannibalism was quite high when different instar larvae interacted each other with maximum cannibalism evidenced in case of 2nd instar v/s 3rd and 4th instar larval treatments compared to late larval instars. Malformation of pupae and deformed adult emergence due to cannibalistic behavior was also revealed during the investigation.

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