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An Efficient Rearing Method for the Fall Armyworm, *Spodoptera frugiperda*, under Crowded Conditions

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Abstract

The fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), is an economically important polyphagous pest, which has recently expanded its distribution from the Americas to over 70 countries. Here, we established an efficient rearing method for *S. frugiperda* under crowded conditions. First, we clarified the larval density at which there is no decrease in survival rate due to cannibalism. *Spodoptera frugiperda* larvae were maintained on an artificial diet till pupation under five density conditions: 10, 30, 50, 70, and 100 individuals per container (5.4L, 26.8 cm × 20.7 cm × 9.8 cm). Survival rates at adult emergence were approximately 70% at density conditions of less than 50, and those in the container with paper towels as refuge were higher than those in the container without paper towels. In the second experiment, two individuals at different developmental stages from 5th instar to pupa were released in a container with or without food, and with or without paper towels, to clarify the developmental stages at which cannibalism occurs. Even when food was present, the individuals without access to refuge during the prepupa were attacked by the 6th instar larva. Our results suggested that conditions which include refuge and moderate density facilitate the rearing of *S. frugiperda* larvae under crowded conditions.

Discipline: Agricultural Environment
Additional key words: cannibalism, density, refuge, Lepidoptera, Noctuidae

Introduction

The fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), which is native to neotropical region, is known as a serious agricultural pest of important crops such as corn, sugarcane, sorghum, and rice (Ashley 1989, Sparks 1979). This insect is a polyphagous pest attacking more than 300 host plants (Montezano et al. 2018). In early 2016, *S. frugiperda* was observed on maize plants in Nigeria, and it has since spread rapidly to other African countries (Cock et al. 2017, Goergen et al. 2016). In 2018, *S. frugiperda* invaded into India and in 2019, it appeared in China and South Korea (Jing et al. 2020, Lee et al. 2020, Sharanabasappa et al. 2018). By 2021, this species had been detected in over 70 countries, including Spain and New Caledonia (FAO 2021). In Japan, it was first found in early July 2019 and had been recorded in all prefectures by 2021 (Wu et al. 2021).

To combat the spread of this insect pest, researchers have attempted to better understand its biological and physiological characteristics, and its insecticide resistance. Based on their findings control strategies against *S. frugiperda*, including pesticides and biological control agents are increasingly being reported (Paredes-Sánchez et al. 2021). Such experimental studies have required a constant and sufficient supply of *S. frugiperda*. Therefore, several recipes for artificial diets including primarily beans and/or corn have been introduced for rearing *S. frugiperda* (Greene et al. 1976, Pinto et al. 2019, Su et al. 2019, Truzi et al. 2021). However, preparing artificial diet is labor intensive, so instead we tried to raise *S. frugiperda* larvae using a commercially available artificial diet for Lepidoptera, the main ingredients of which are mulberry leaves and soybean.

The important challenge for rearing immature individuals of *S. frugiperda* is to reduce mortality until adult emergence. Because *S. frugiperda* are naturally cannibalistic (Chapman et al. 1999a, 2000), researchers

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often rear *S. frugiperda* larvae separately in well plates or glass tubes, which is highly labor intensive (He et al. 2021, Jin et al. 2020). In the present study, therefore, we examined the effects of larval rearing density on their survival and development, and, in order to establish an efficient method for rearing larvae using an artificial diet under crowded conditions, investigated the effects of refuge to prevent cannibalism.

Materials and methods

1. Insects

The original *S. frugiperda* eggs were collected in a corn field at the Kyushu Okinawa Agricultural Research Center, NARO, Kumamoto Prefecture (32°87′94″N, 130°74′30″E) in Japan in 2019. Larvae were reared on an artificial diet, Insecta LFS® (Nosan Corporation, Yokohama, Japan) at 27 ± 1°C under a 14:10 h light/dark cycle in the laboratory. Insecta LFS® is a commercially available diet for rearing Lepidopteran and Coleopteran insects, made of mulberry leaves, soybean, starch, sugar, vitamins, minerals and so on, and is sausage-shaped with a diameter of 5.0 cm. The rearing temperature was determined based on a previous report that the optimal temperature for rearing *S. frugiperda* is 27°C by Su et al. (2019).

2. Experiment 1, The effect of density and refuge availability on survival

The egg mass was put into a plastic container (0.86 L, 15.8 cm width × 11.9 cm depth × 4.6 cm height) with approximately 15 g of the artificial diet until the second instar larval stage. The second instar larvae at the time of head capsule slippage, indicating the pre-molting, were transferred into a rectangular plastic container (5.4 L, 26.8 cm width × 20.7 cm depth × 9.8 cm height) with a piece of Kimtowel® paper towel (PT) (a commonly used product in Japan consisting of four thin papers; Nippon Paper Crecia, Tokyo) laid on the bottom (Fig. 1). Then, 70 g of the diet cut into 3 equal portions was added to the container, which was covered with a lid having a ventilation hole with a nylon mesh. The density of individuals was 10, 30, 50, 70 or 100 larvae per container. To verify the effect of refuge on the survival rate and developmental periods, three pieces of PT were gently stacked over the larvae and diets, with their edges rolled up to create space between each PT and those above or below it (Fig. 1A). As controls, we also prepared containers in which the larvae and diets were not covered with pieces of PT, for each density (Fig. 1B). Each treatment was replicated 5 times. Diets were changed every 3 days. Pupation and adult emergence were checked once a day. After pupation, individuals were transferred into plastic cups with moistened cotton to protect them from drying, and maintained individually until adult emergence. On the 4th day after pupation, individuals were separated by sex, and pupal weight was determined with a balance.

To estimate of the effects of rearing density and PT treatment on the survival rate until pupation or emergence, logistic regression analysis was performed, where, to avoid the unstable results due to the existence of zero-cells, all cells were added 0.5 (Haldane-Anscombe correction), was performed on the data beforehand. If significant difference on density x PT interaction was observed, logistic regression analysis was re-analyzed by treatment and hereafter, a *G*-test with Bonferroni correction was conducted as the post-hoc test. To estimate the effects of rearing density, PT treatment, and sex on the larval or pupal development period and pupal weight, three-factor ANOVA was performed. When some interactions were observed, if necessary, simple-main-effect test was conducted as the post hoc test.

3. Experiment 2, The effect of food and refuge availability on cannibalism

Because older larvae cannibalize more frequently than younger ones (Chapman et al. 1999b), we investigated cannibalism in the 5th instar larva, the 6th (last) instar larva, prepupa and pupal stages. We released two individuals at different stages ranging from the 5th instar larva to pupal stage in a transparent container (15.0 cm in height by 8.0 cm diameter). Under crowded conditions, the discrepancy in age between individuals is usually within a few days, and most of the individuals encountered by L6D0 were L5D0, 5HCS, L6D0 or

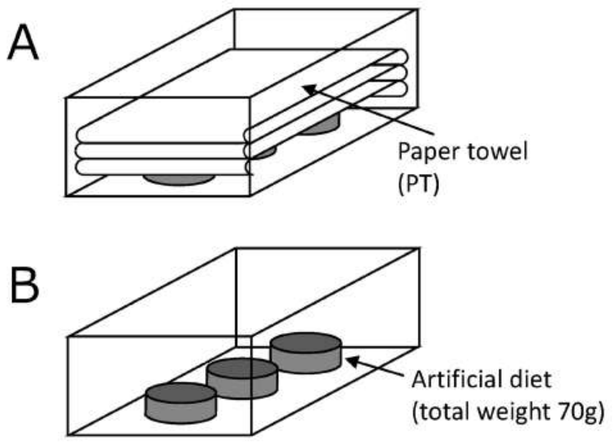

Fig. 1. Treatments used in Experiment 1 to evaluate the effects of larval density and paper towels on the survival of *Spodoptera frugiperda*

L6D2, and L6D2 individuals encountered individuals in the L6D0, L6D2, Prepupa and Pupa (see Table 1 for an explanation of stage abbreviations). Therefore, the following seven combinations of individuals each were released in separate containers: L6D0 vs L5D0, L6D0 vs 5HCS, L6D0 vs L6D0, L6D0 vs L6D2, L6D2 vs L6D2, L6D2 vs prepupa and L6D2 vs pupa (see Table 2 for the combinations).

To assess the effect of the presence of the refuge and/or the diet on the tendency to cannibalize, the experiments were executed under each of the following four conditions: the diet alone, the diet and three pieces of PT, three pieces of PT alone, and neither diet nor PTs (Fig. 2). The diet was added as an approximately 5.0 g piece. The PTs were placed in the same manner as in Experiment 1. At 24 h after release, we recorded the numbers of cases in which individuals in the experiment remained alive as an index of cannibalism. All treatments were replicated 15 times. All experiments were performed in a room at 27 ± 1°C under a 14:10 h light/dark condition.

In observations, most of L6D0 and L6D2 individuals were not killed. Therefore, for each of L6D0 and L6D2, the logistic regression analysis was performed to estimate

Table 1. Abbreviations of developmental stages in Experiment 2

Abbreviation	Developmental stage
L5D0	0-day-old, fifth instar larva
5HCS	an individual at head capsule slippage during molting to the sixth instar larval stage
L6D0	0-day-old sixth instar larva
L6D2	2-day-old sixth instar larva
prepupa	a metamorphic individual prior to the pupal stage
pupa	1-day-old pupa

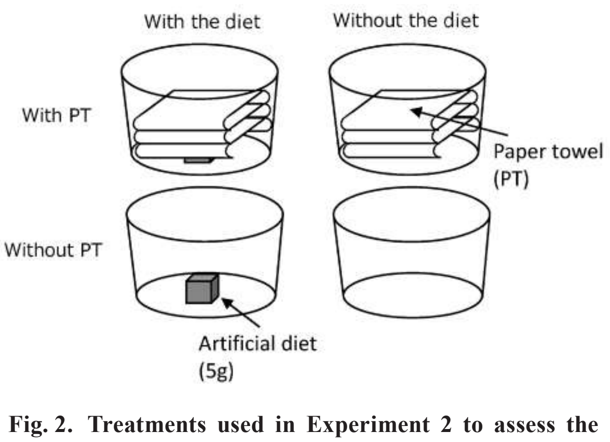

Fig. 2. Treatments used in Experiment 2 to assess the cannibalism between two individuals of *S. frugiperda*

the effects of the food, PT, and the larval stages in the proportion of survived individuals of the opponent. To avoid unstable results due to the existence of zero-cells, Haldane-Anscombe correction was performed on the data beforehand. Evaluation by model selection was adopted instead of the significance test, for the lack of the balance between sample size and the number of stage combinations. The best model was then decided by the forward-backward stepwise selection method. All statistical analyses were performed using SAS OnDemand for Academics 3.8 (SAS Institute 2020).

Since Experiment 1 resulted in low mortality in the 50-individual density condition, the insects for this experiment were reared at a density of 50 individuals. To analyze the relationship between body size and cannibalism, the head capsule width of larvae and body weight of individuals were measured at each developmental stage as indices of body size. The head capsule width and body weight were analyzed by using the Tukey-Kramer honestly significant difference test with R version 4.0.2 software (R Developmental Core Team).

Results

1. Experiment 1, The effect of density and refuge availability on survival

During this experiment, the number of individuals had decreased compared to the start of the experiment, because few dead larvae were found, but several larvae were attacked by the other individuals in the container. Therefore, we determined that the most of death in this experiment was due to cannibalism rather than starvation.

The survival rates at both pupation and adult emergence tended to decrease with density (Fig. 3). Although larvae were put on the diet at the beginning of the experiment, they actively dispersed over or between PTs except when feeding, and they hid between PTs especially during molting. In the treatments with PTs, the survival rate at pupation under the 70-individual density condition was significantly lower than those under density conditions of less than or equal to 50 individuals, followed by the 100-individual density condition ($P < 0.01$, Fig. 3A). Pupation rates in the treatments without PTs were not significantly different between the density conditions with 10 and 70 individuals, but the pupation rates under the 100-individual density conditions were significantly lower than those under the other conditions ($P < 0.01$, Fig. 3A). The adult emergence rates under the 100-individual density condition were significantly lower than those under the density conditions of less than or equal to 70 individuals in both treatments

(P < 0.01, Fig. 3B). Overall, the survival rates in the treatment without PTs were lower than those in the treatment with PTs. Pupation rates under the 30-, 50- and 100-individual density conditions differed significantly between the treatments with PTs and without (P < 0.01, Fig. 3A). The adult emergence rates differed significantly between the treatments with and without PTs under both the 30- and 50-individual density conditions (P < 0.01, Fig. 3B).

For larvae reared, the developmental period under the 100-individual density condition, was significantly longer, regardless of the presence of PTs, than those under the other four density conditions (P < 0.01, Fig. 4A).

Regarding the pupal developmental period in the treatment with PTs, the 100-individual density condition had the longest. In the absence of PTs, the differences in pupal developmental period among the five conditions were not significant (P > 0.01, Fig. 4B).

As for pupal weight, females in the treatment with PTs under the 100-individual density condition had significantly lighter pupal weights than those under the other conditions, followed by those under the 10-individual density condition (P < 0.01, Fig. 5A). In the treatment without PTs, females under the 10- and 100-individual density conditions were significantly lighter than those under the 70-individual density condition (P < 0.01, Fig. 5A). The pupal weights of males under the 30-, 50- and 70-individual density conditions were significantly heavier than those under the 10- and 100-indvidual density conditions (P < 0.01, Fig. 5B). The pupal weights of males in the treatment without PTs were similar to those for females under the same treatments. The pupal weights in the treatment with PTs were significantly heavier than those without PTs under the 30- and 50-individual density conditions for females, and under the 30-individual density condition for males (P < 0.01, Fig. 5).

2. Experiment 2, The effect of food and refuge availability on cannibalism

In the cases encountered with L6D0, the existence of food and a part of larval stages were selected as valid variables for explaining cannibalized or not by stepwise regression (food: P < 0.0001; L5D0: P < 0.0001; 5HCS: P < 0.0001), whereas PT and food were chosen as the parameters by stepwise model selection (PT: P = 0.0003; food: P = 0.0139). The proportion of survived individuals in the combinations of L6D0 vs L6D0 was over 90% and few were killed in the four treatments (Table 2). None of individuals were not cannibalized for the two combinations of L6D0 vs L6D2, and L6D2 vs L6D2 in all treatments. On the other hand, the proportion of survived individuals in L5D0 treated with no diet and no PTs was lower than by the other three treatments. With regard to the combination of L6D0 vs 5HCS, the proportion of survived individuals in the two treatments without the diet were lower than those in the two treatments with the diet. In the combination of L6D2 vs prepupa, although

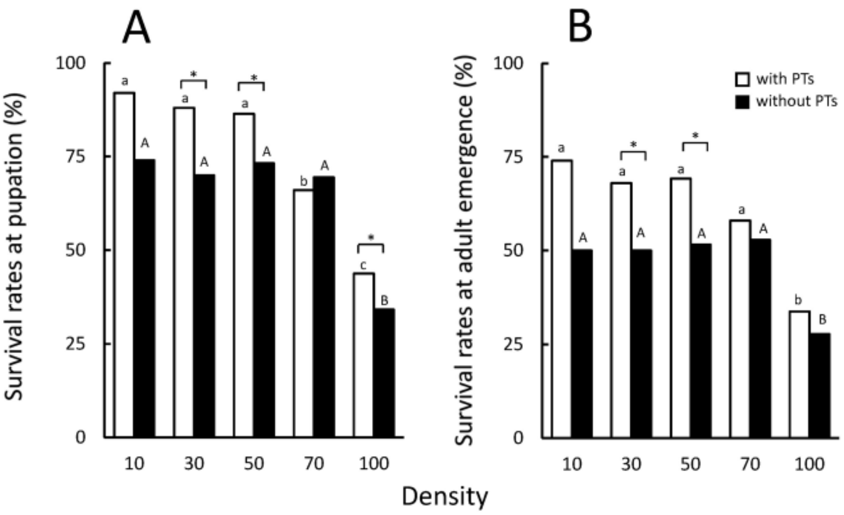

Fig. 3. Survival rates at pupation (A) and adult emergence (B) in *S.frugiperda* reared under five different density conditions
The horizontal axis means the number of individuals per container (5.4 L). Results indicated by the same lower-case letter or upper-case letter were not significantly different on the comparison among rearing densities in the treatment (P > 0.01, Bonferroni correction). Asterisks indicate a significant difference between the two treatments (P < 0.01).

it was not selected for model selection due to the lack of sample size, the proportion of survived individuals of prepupa in the two treatments with PTs were higher than those in the two treatments without PTs, and the proportion of survived individuals of prepupa in the treatment with no diet and no PTs was the lowest among all treatments. Most of the individuals in the combination of L6D2 vs pupa did not die.

The head capsule width of 5th instar larvae was not significantly different between L5D0 and 5HCS, whereas the body weight of the latter was more than four times that of the former ($P < 0.05$, Table 3). Similarly, there were no

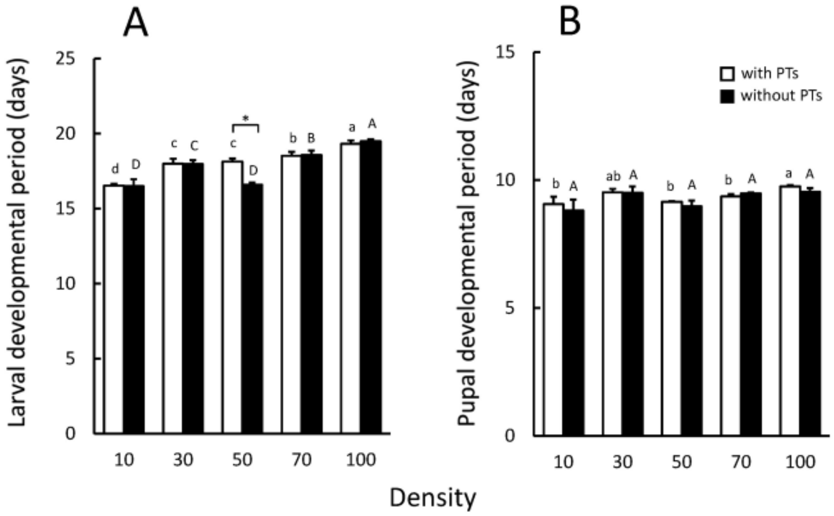

Fig. 4. Developmental period from hatching to pupation (A) and from pupation to adult emergence (B), in the individuals reared under the five different density conditions

Values are means ± SE. Results indicated by the same lower-case letter or upper-case letter were not significantly different on the comparison among rearing densities in the treatment ($P > 0.01$, Bonferroni correction). Asterisks indicate a significant difference between the two treatments ($P < 0.01$).

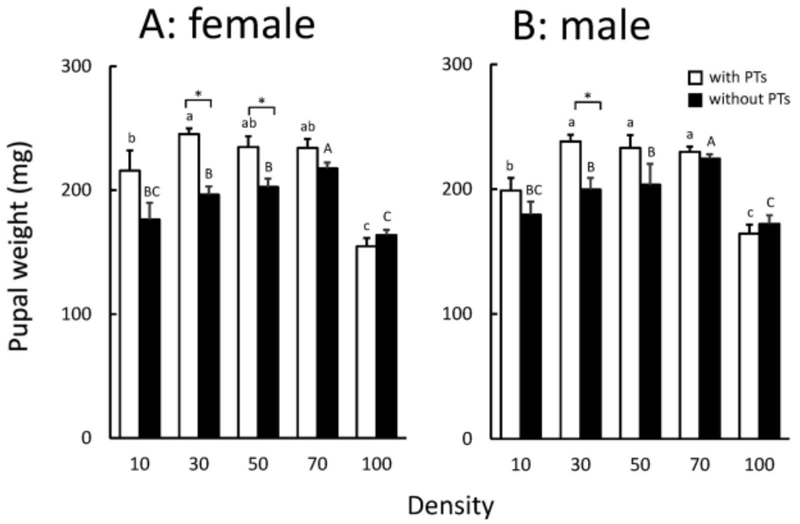

Fig. 5. Pupal bodyweight of individuals of each sex reared under the five different density conditions

Values are means ± SE. Results indicated by the same lower-case letter or upper-case letter were not significantly different on the comparison among rearing densities in the treatment ($P > 0.01$, Bonferroni correction). Asterisks indicate a significant difference between the two treatments ($P < 0.01$).

Table 2. The proportion of survived individuals (%) of *S. frugiperda* under four different conditions at 24 hours after release into the container

Combination	Developmental stage	With the diet		Without the diet*,**	
		Without paper towels**	With paper towels	Without paper towels	With paper towels**
L6D0 vs L5D0	L6D0	100	100	100	100
	L5D0*	73	100	33	73
L6D0 vs 5HCS	L6D0	100	100	100	100
	L5HCS*	100	93	0	20
L6D0 vs L6D0	L6D0 (I)	100	100	100	100
	L6D0 (II)	100	100	100	93
L6D0, vs L6D2	L6D0	100	100	100	100
	L6D2	100	100	100	100
L6D2 vs L6D2	L6D2 (I)	100	100	100	100
	L6D2 (II)	100	100	100	100
L6D2 vs Prepupa	L6D2	100	100	100	100
	Prepupa	53	100	0	86
L6D2 vs Pupa	L6D2	100	100	100	100
	Pupa	100	100	86	100

* represents the factors selected by forward-backward stepwise regression method in combinations with L6D0.
** represents the factors selected by forward-backward stepwise regression method in combinations with L6D2.

significant differences in head capsule width of 6th instar larvae among L6D0, L6D2 and prepupa stages ($P > 0.05$, Table 3). The body weights of pupa were significantly smaller than those of prepupa ($P < 0.05$, Table 3).

Discussion

In our present study, by comparing the developmental period, we found that the 70- and 100- individual density conditions delayed development. Chapman et al. (1999a) described that cannibalism increases with the degree of crowding in *S. frugiperda*. Our finding might have been related to the fact that individuals under high density conditions are susceptible to cannibalism and the amount of food per larva decreased. In addition, under the 50-individual density condition in the treatment with PTs, we were able to rear individuals until adult emergence with the survival rates of approximately 70%. Also, implying that the existence of the PTs facilitated survival, the treatment with PTs suppressed mortality compared to the treatment without PTs under the 30- and 50-individual density conditions. In a study by Silva and Parra (2013), 40 individuals were reared in a container filled with 200 mL of an artificial diet and approximately 90% survived; the larvae burrowed into the large piece of diet to prevent cannibalism. Thus, a refuge as the stacked PTs or food, is important not to reduce the survival rate of *S. frugiperda* larvae.

The pupal weight varied among the five density-conditions, with the 100-individual density having the lowest pupal weight among the conditions for both females and males. In the 100-individual density condition, there was almost no food left in the container at the time of food change. By contrast, the conditions showing comparatively heavy bodyweight were the density conditions with 30, 50 and 70 individuals. The average values of bodyweight in the treatment with PTs were higher than those without PTs, except under the 100-individual density-condition. These results might have been attributable to the additional effect of cannibalism and sufficient diet. Since the probability of encountering other larvae increased in the treatment without PTs, the behavior by which larvae avoided other individuals would have interfered with the feeding diet, leading to lighter pupal body weight than in the treatment with PTs. Experiment 1 revealed that the PTs had a positive effect on body weight under the conditions in

Table 3. Head capsule widths and body weights (mean ± SD) of each developmental stage

Developmental Stage	Head capsule width (mm)	Body weight (mg)
5th larva, day 0	1.8 ± 0.1b	29.5 ± 6.7e
5th larva, head capsule slipage	1.9 ± 0.1b	138.3 ± 16.6d
6th larva, day 0	2.6 ± 0.1a	119.8 ± 19.3d
6th larva, day 2	2.6 ± 0.1a	443.5 ± 74.1a
Prepupa	2.7 ± 0.1a	257.3 ± 23.5b
Pupa	-	223.2 ± 23.6c

Values are means ± SD. The significance of differences in the mean values in each column were analyzed using Tukey-Kramer HSD test ($P < 0.05$).

which there was a sufficient amount of food.

In terms of whether the artificial diet used in the present study was suitable, the results of pupal weights will be discussed. The average pupal weights under the 50-individual density condition with PTs were 234.8 mg for females and 233.0 mg for males, which are similar to pupal weights in the previous reports. For instance, Montezano et al. (2019) reported that the average pupal weights were 230.5 mg for females and 189.7 mg for males when the individuals were reared on an artificial diet at 25°C, and Jin et al. (2020) described that the pupal weights of *S. frugiperda* reared on corn leaves at 25°C were 200.0 mg for females and 199.1 mg for males. Therefore, we determined that the Insecta LFS® used in the present study has sufficient nutritional value for rearing *S. frugiperda*.

In Experiment 2, we had expected that cannibalism would occur in the combination of L6D0 and L6D2 due to the large weight difference. However, neither of the larvae died in that combination, although some larvae bit or threatened the other individuals with their mandibles. The reason for this may be that the 6th instar larvae avoid attacking individuals that have mandibles of the same size, because this would expend more energy. In contrast, L6D0 cannibalized L5D0, who had smaller head capsules. Consequently, our results demonstrated that the difference in head capsule width is more important than the difference of body weight for cannibalism between larvae. Therefore, to reduce the chance of cannibalism under rearing environment, it is important not to place larvae of widely different instar in the same container. With regards to inter-molting larva, Dial and Adler (1990) mentioned the inter-molting larvae of *Helicoverpa zea* (Lepidoptera: Noctuidae) are exposed to a high risk of cannibalism because they are not able to cannibalize other larvae. The results of our experiments, in which individuals at the stage of head capsule slippage were attacked by L6D0 under the condition without the diet, support the previous studies mentioned above. On the other hand, prepupa were vulnerable to be attacked by L6D2 under the condition without PTs. In the corn field, *S. frugiperda* larvae do not usually encounter other individuals, because larvae feed inside leaf whorls and pupate in the soil (Labatte 1993, Morrill & Greene 1973, Sparks 1979). In our present rearing container, they prefer to hind in PTs or food instead of leaves before pupation, and it appeared to be difficult for the cannibal larvae to find prepupa that were hiding in PTs and not actively moving. Besides, most of pupae were not attacked by larvae despite the difference of body size, showing that pupae after hardening are less susceptible to cannibalism even under circumstances without food. Thus, our results indicated that the differences in ages and the existence of hiding places are closely related to the survival of individuals except the pupa which have hard body surfaces, under crowded conditions.

From the above discussion, if *S. frugiperda* are to be raised using the same amount of artificial diet and the same containers as in this study, the 50-individual density condition is recommended, where it is concluded that refuge material such as PT facilitates the rearing of *S. frugiperda* larvae under crowded conditions.

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