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Effect of Diet on the Longevity and Oviposition Performance of Black Soldier Flies, *Hermetia illucens* (Diptera: Stratiomyidae)

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Abstract

We examined the nutritional value of different diets on the longevity and reproductive performance of black soldier flies (*Hermetia illucens*) under laboratory conditions. In addition to water only (W) (control group), four diets were used: sugar and water (SW); pollen, sugar, and water (PSW); pollen, honey, and water (PHW); and honey and water (HW). The PSW group exhibited the highest reproductive performance because it had the longest oviposition period, largest number of clutches and hatched clutches, largest number of eggs laid/female, and greatest male and female longevity. Nevertheless, the highest hatching rate was found in the SW group. The number of successfully hatched eggs (fertilized) was the greatest in the PSW and HW treatments, but the differences between diets (SW, PSW, PHW, and HW) were nonsignificant.

Discipline: Biomass Utilization
Additional key words: food supply, rearing method, reproductive performance

Introduction

The black soldier fly (BSF), *Hermetia illucens* (L.), is a true fly (Diptera) of the family Stratiomyidae. It was native to America but is now present in tropical and temperate regions worldwide (Wang & Shelomi 2017). BSF adults do not harm humans and do not transmit any human diseases (Čičková et al. 2015, Sheppard 2002). The larvae feed on various organic materials and have been used to manage manure (Sheppard 1983, Yu et al. 2009), fecal sludge (Banks et al. 2014, Lalander et al. 2013), distillery grain waste (Webster et al. 2015), food waste, rice straw (Green & Popa 2012, Zheng et al. 2012), and kitchen waste (Nguyen et al. 2014).

Caligiani et al. (2018) and Barragan-Fonseca et al. (2017) reported that BSF larvae are a good source of proteins (37%-63% dry matter) and fat (7%-39% dry matter) for animal diets. The BSF also has great utility in the feed and food industry (Borgogno et al. 2017), in addition to the production of biodiesel (Feng et al. 2018) and biodegradable bioplastics (Barbi et al. 2019). Moreover, BSF feces can be used as fertilizer for rice (Wu et al. 2020).

However, the main problem in producing larvae for any application involves scaling up production capacity, which requires a thorough knowledge of the fly's biology, to enhance egg production (Čičková et al. 2015). The goal of insect rearing is to produce the greatest number of insects in the least time, as inexpensively as possible. To develop a large-scale rearing method for BSF, studying its reproductive biology is necessary, as well as collecting many fertilized eggs for larval growth.

Holmes et al. (2012) reported that larval feeding conditions directly impact pupal development, adult life span, fecundity, and egg viability. As larval growth depends on diet composition, food ratio, and feeding frequency, it is necessary to establish the optimal levels of these parameters (Kim et al. 2011).

Several studies reported that food quality greatly influences life history traits, such as the survival, development, and fecundity of insects in nature (Adams 1999, Davey 1967, Dittman & Biczkowski 1995, Joern & Behmer 1997, Wheeler 1996). To understand the biology of the adult BSF, such information is necessary. Tomberlin & Sheppard (2002) reported that *H. illucens* adults do not need to feed but that their life spans are substantially

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extended when provided with water. Nakamura et al. (2016) reported that adult flies survived longer when water was supplemented with sugar. Subsequently, Bruno et al. (2019) and Lupi et al. (2019) reported that feeding of sugar solution not only increased the egg production of adult females but also extended their life spans. The adult BSF feed on rich protein diets to maximize oviposition and longevity (Bertinetti et al. 2019). They also preferred feeding on honey compared to white sugar, brown sugar, or water (Romano et al. 2020) while using a white color background.

In the present study, the BSFs were reared on four different diets in wire-framed polyethylene cages with lighting from light-emitting diodes (LED). The objective of this study was to determine the influence of different diets on egg production parameters and assess adult fly longevity under different artificial diets. Additionally, we examined the life history parameters of adult BSF, including fecundity and hatchability, under different conditions.

Materials and methods

1. Flies

Adult BSFs (*H. illucens*) (Diptera: Stratiomyidae) were obtained from a colony that Dr. Nakamura established with specimens collected at the Japan International Research Center for Agricultural Sciences, Tsukuba, Japan, in 2013.

2. Rearing procedures

Rearing cages, water cases, and oviposition cases followed those of Nakamura et al. (2016). The flies were reared in wire-framed polyethylene cages (27 cm × 27 cm × 27 cm) with nylon mesh on two sides; polyethylene sheets on the top, bottom, and front; and a tarpaulin on the back. Water was provided with two water cases (3.4 cm × 6.4 cm × 1.5 cm) plugged with cotton, and the nylon mesh sides of the cages were sprayed with tap water three times a day. An oviposition case (16 cm × 12 cm × 3 cm) with a lid that had four holes (2 cm in diameter) was placed in each cage. It was covered with nylon mesh to allow oviposition, but not entry. Thick paper, folded in half (ca. 6 cm high), was placed inside each cage with a paper towel as an oviposition substrate to collect eggs. Paper towels were crumpled to facilitate counting of eggs (Nakamura et al. 2016), as opposed to corrugated cardboard used in other studies (Sheppard et al. 2002, Tomberlin & Sheppard 2002, Zhang et al. 2010).

During oviposition, the residue of the artificial diet consumed by the larvae in a case encouraged oviposition. The eggs were collected and placed in a Petri dish (9 cm in diameter, 2 cm high), and it was firmly sealed to prevent larval escape. The fertilized eggs were kept in a 500-mL Erlenmeyer flask with an artificial diet for two weeks. Then, the hatched larvae were transferred to a plastic container (20 cm × 15 cm × 7 cm) covered with a ventilated lid. They were kept on an artificial diet until about 80% turned dark brown (prepupae). The prepupae were transferred again to a large plastic container (28 cm × 22 cm × 10 cm) that held dried coffee grounds as a soil substitute in which larvae could pupate. The newly emerged adults were transferred to another wire-framed polyethylene cage (27 cm × 27 cm × 27 cm) containing an oviposition case.

Two 40-W fluorescent lamps (FLR40SEX-W/M/36-HG, NEC, Tokyo, Japan) were positioned ~10 cm above the cages, which were illuminated from 06:00 to 22:00. One 20-W LED lamp (400 nm-800 nm with peak emissions at 451 nm and 555 nm; JIM-LTG20W, Jinxing Rantoon Co. Ltd., China) was also suspended ~5 cm above each cage; it was turned on from 09:00 to 15:00. These artificial light sources were used in the oviposition and longevity experiments for all diet treatment experiments.

The experiments were conducted under 60% ± 10% RH, with a 16-h light/8-h dark photoperiod at 25°C ± 1°C. The ingredients of the artificial diets for the BSF larvae were as follows: 25-g dried yeast (Asahi Food and Healthcare Co. Ltd., Japan), 250-g wheat germ (Nisshin Flour Milling Co. Ltd., Japan), 150-g rabbit and guinea pig diet (RC4, Oriental Yeast Co. Ltd., Japan), and 750-mL distilled water. The treatments were checked every day at 16:00.

3. Oviposition and longevity under different diets

In the present study, we examined and compared the oviposition and longevity of adults of both sexes among the artificial diets, including water only (W) (control); sugar and water (SW); pollen (Arysta LifeScience Corporation), sugar (sucrose), and water (PSW); pollen, honey, and water (PHW); and honey and water (HW). There were different modes of feeding on each diet. For instance, water was provided by supplying 20 mL of distilled water in cotton in a plastic case (3.4 cm × 6.4 cm × 1.5 cm). Sugar was provided as a sugar cube, pollen as 1 g of pollen grains on a plastic Petri dish (4 cm in diameter, 1.5 cm high), and honey as 8-mL solution in cotton.

Equal numbers of newly emerged male and female adults (n = 20) (< 17 h) were released into the wire-framed polyethylene cages (27 cm × 27 cm × 27 cm). Two 40-W fluorescent lamps and a 20-W LED lamp were suspended above.

Oviposition period (day) was defined as the period from the first egg to the final egg laid. The eggs deposited were counted as the number of egg clutches. Longevity was determined as the number of both sexes alive every day for each treatment at 16:00. The numbers of egg clutches were counted based on their color differences and locations on a crumpled dry paper towel, although some clutches were clustered. Four days later, their hatching rate was determined by counting the number of eggs per clutch and the number of hatched eggs per treatment. Oviposition was evaluated by counting the number of eggs per clutch. The clutches were soaked in 70% ethanol to separate the eggs for counting and photographing under a microscope. Then, the eggs were counted in the photographs.

Hatchability was calculated as the number of hatched clutches divided by the total number of clutches. The fertilized eggs were counted from successfully hatched clutches. To determine longevity, dead flies were counted daily. Each treatment comprised 10 replicates (10 cages).

4. Statistical analysis

The differences in oviposition performance, egg numbers, longevity, hatchability, and mean total egg clutch number among the different dietary treatments were analyzed using the analysis of variance and Tukey's honestly significant difference test after ANOVA. The R software version 3.5.0 was used (R Core Teams 2018).

Results

1. Longevity and fecundity of the BSF under different diets

Male survivorship was higher than that of female in all treatments (Fig. 1). The longevity of both male and female BSF on water (control) was lower than for flies on diets. The longest longevity of both male and female flies occurred in the PSW treatment.

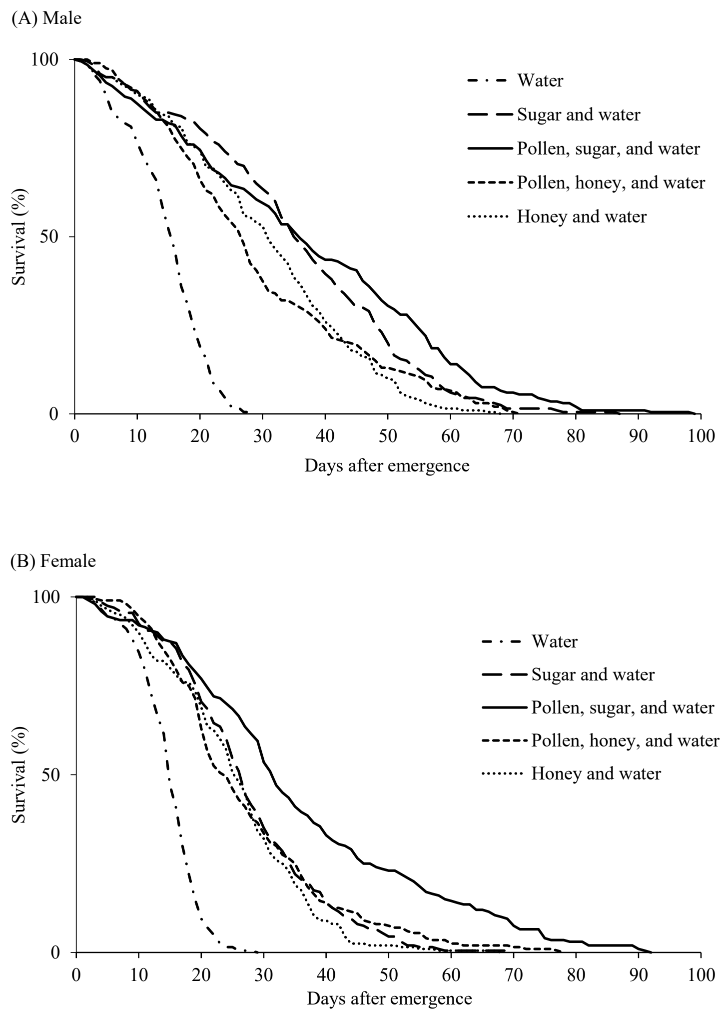

Fig. 1. Survival curves of black soldier flies (*Hermetia illucens*) under various diets with lighting from LED lamps only
(A) Male (n = 10); (B) Female (n = 10)

The peak of oviposition was recorded on the 7th day after emergence in controls. The total number of egg clutches (hatched egg clutches) was 16.7 (0), with oviposition duration of 4-12 days (Fig. 2A). Oviposition peaked in the SW and PSW treatments on the 6th day after emergence. In the SW treatment, the total number of clutches (hatched egg clutches) was 35.6 (8.2), with an oviposition duration of 16-33 days. In the PSW treatment, the total number of clutches (hatched egg clutches) was 49.1 (9.4), with oviposition duration of 25-66 days (Fig. 2B, C). In the PHW treatment, the oviposition peak occurred on the 5th day after emergence; the total number of clutches (hatched egg clutches) was 43.8 (8.5), with an egg laying duration of 25-46 days (Fig. 2D). In the HW treatment, the total number of clutches (hatched egg clutches) was 41.9 (8.6) for an oviposition duration of 14-33 days, and the peak of oviposition was on the 7th day (Fig. 2E).

2. Life history attributes of adult BSF under different diets

The life history parameters of adult BSF under different dietary treatments are shown in Table 1. Males lived longer than did females. Among the males, the controls had the shortest life spans (mean ± standard error [SE]: 16.06 ± 0.43 days), and the longest life spans occurred in the PSW group (38.39 ± 1.86 days). The life spans for the SW, HW, and PHW treatments were 36.72 ± 1.46, 31.73 ± 1.41, and 30.67 ± 1.10 days, respectively. Contrarily, the longest and shortest female life spans were recorded in the PSW (37.07 ± 2.75 days) and control groups (15.94 ± 0.34 days), respectively. Other treatments did not significantly differ.

The durations of oviposition for the various diets were as follows: W, 8.40 ± 0.66 days; SW, 23.00 ± 1.73 days; PSW, 36.00 ± 4.07 days; PHW, 35.40 ± 2.47 days; and HW, 25.50 ± 1.91 days.

The greatest number of clutches per female was recorded in PSW (2.46 ± 0.09), followed by PHW (2.19 ± 0.12), HW (2.09 ± 0.23), SW (1.78 ± 0.16), and W (0.84 ± 0.09). In the control group, no clutches hatched. The number of hatched clutches did not significantly differ among the four different diet treatments. The minimum mean number was 0.41 ± 0.07 in the SW treatment, and the maximum was 0.47 ± 0.05 in the PSW treatment.

The number of eggs per female also did not significantly differ among the treatments. The largest number of eggs was found in the PSW treatment (1,289.08 ± 175.29; range: 774-1,871 eggs), and the lowest number occurred in the controls (504.60 ± 63.84; range: 156-767 eggs). None of the eggs in the control females were fertilized, whereas those in the other groups were as follows: SW, 280.19 ± 62.94 eggs (range: 619-1,924); PSW, 313.07 ± 70.33 eggs (range: 774-1,871); PHW, 267.39 ± 44.03 eggs (range: 888-2,115); and HW, 318.50 ± 56.12 eggs (range: 620-1,437).

The highest percentage of hatchability was recorded in the SW treatment (24.22% ± 3.48%), followed by HW (22.29% ± 3.87%), PSW (19.11% ± 2.28%), and PHW (19.11% ± 2.20%). However, there were no significant differences in hatchability among the dietary treatments. Nevertheless, the highest hatchability occurred in the SW treatment.

Discussion

We demonstrated small-scale rearing of BSF, *H. illucens* (L.) and determined the effect of diets on longevity and oviposition performance for each treatment. In BSF, sugar feeding is crucial for longevity (Bruno et al. 2019, Nakamura et al. 2016). Egg production and longevity varied among the dietary treatments. The flies that fed on SW, PSW, PHW, and HW outperformed those given only W (controls). Among the different diets, the flies fed with PSW survived longer than those receiving other diets. Among the treatment groups, longevity varied from 67 to 98 days. The number of eggs appeared to increase during the first week. According to Hagen (1950), the highest number of eggs was produced during the first days of oviposition. However, in this study, some females produced the greatest number of eggs very close to the end of the oviposition period.

The maximum daily egg production for all treatments was observed on the 5-7th day after emergence. Bertinetti et al. (2019) reported that the maximum daily egg production occurred on the 5th day after emergence for flies that received no diet (control), drinking water, a mix of sugar, bacteriological peptone, milk powder (milk), or agar with sugar (agar). The number of clutches per female did not significantly differ between the PSW and PHW treatments. The highest number of hatched clutches per female occurred in the PSW treatment; however, it did not significantly differ from those of the other treatments. The number of eggs per female was more than twice as high in all diets as in controls (W). The number of eggs per female ranged from 156 to 767 in the control group, 619 to 1,924 in the SW group, 774 to 1,871 in the PSW group, 888 to 2,115 in the PHW group, and 620 to 1,437 in the HW group. The number of eggs laid per female was higher than that reported in previous studies, which ranged from 300 to 1,200 eggs (Nakamura et al. 2016), 500 to 1,000 eggs (Furman et al. 1959), 119 to 502 eggs (Gonzalez et al. 1963), and 205 to 820 eggs (Stephens 1975).

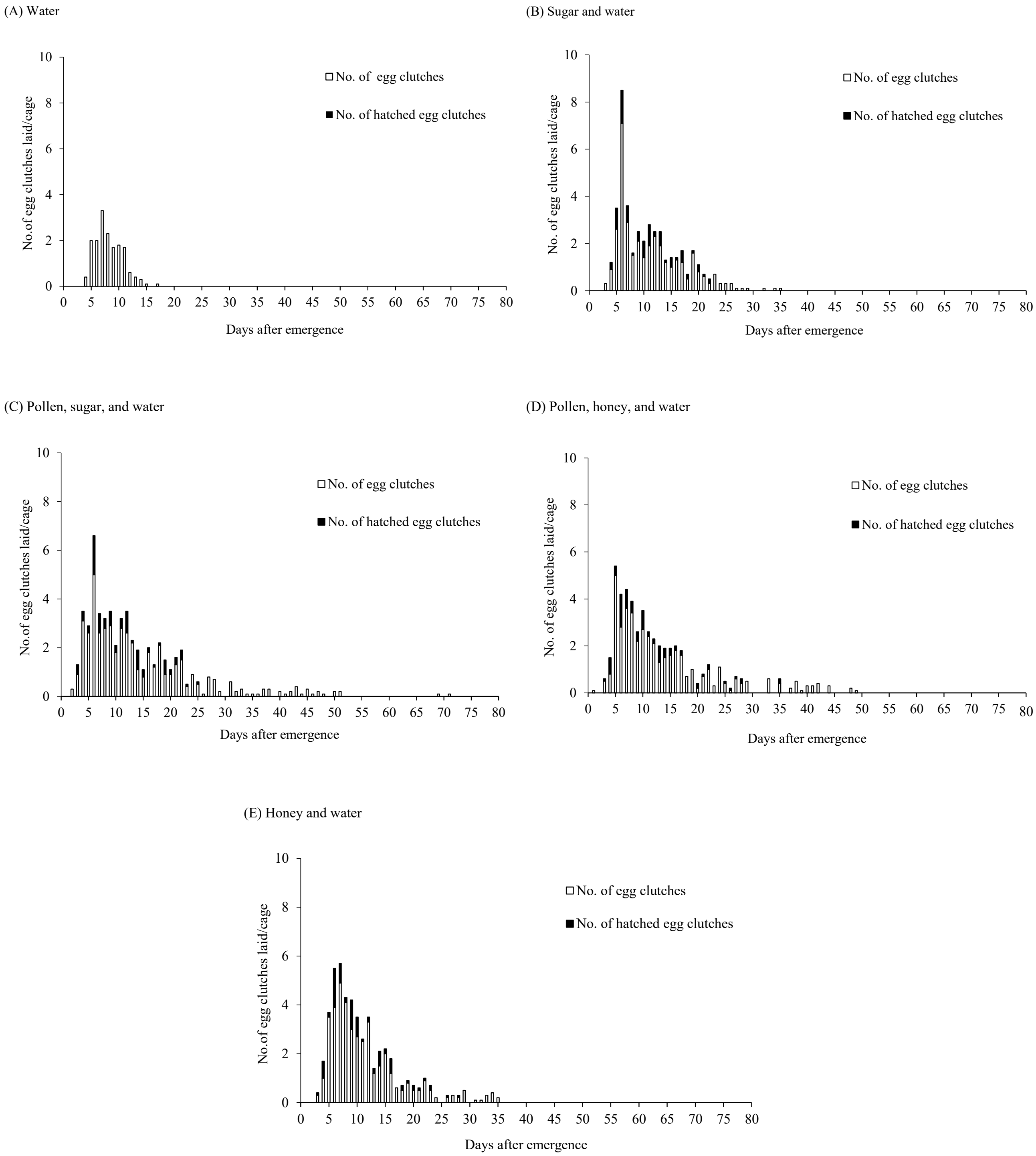

Fig. 2. Numbers of clutches laid by black soldier flies (*Hermetia illucens*) under various diets and lighting with LED lamps only

(A) Water only: W (n = 10); (B) Sugar and Water: SW (n = 10); (C) Pollen, Sugar, and Water: PSW (n = 10); (D) Pollen, Honey, and Water: PHW (n = 10); and (E) Honey and Water: HW (n = 10)

Table 1. Life history parameters of adult black soldier flies (*Hermetia illucens*) on various diets under fluorescent and LED light[a]

Life-history parameter	Diets[b]					ANOVA		
	W (Control)[c]	SW[c]	PSW[c]	PHW[c]	HW[c]	*F*	*P*	*n*[d]
Male longevity (day)[f]	16.06 ± 0.43a	36.72 ± 1.46cd	38.39 ± 1.86d	30.67 ± 1.10b	31.73 ± 1.41bc	42.2986	< 0.0001	200
Female longevity (day)[f]	15.94 ± 0.34a	28.64 ± 1.15b	37.07 ± 2.75c	28.36 ± 1.73b	26.95 ± 1.28b	20.2925	< 0.0001	200
Oviposition period (day)[f]	8.40 ± 0.66a	23.00 ± 1.73b	36.00 ± 4.07c	35.40 ± 2.47c	25.50 ± 1.91b	21.2478	< 0.0001	10
No. of clutches/female[f]	0.84 ± 0.09a	1.78 ± 0.16b	2.46 ± 0.09c	2.19 ± 0.12bc	2.09 ± 0.23bc	17.7321	< 0.0001	10
No. of hatched clutches/female[f]	0.00 ± 0.00a	0.41 ± 0.07b	0.47 ± 0.05b	0.43 ± 0.06b	0.43 ± 0.06b	11.9769	< 0.0001	10
No. of eggs/female[f]	504.60 ± 63.84a	1,159.56 ± 136.24b	1,289.08 ± 175.29b	1,163.53 ± 133.58b	1,060.86 ± 84.17b	6.0443	0.0005	10
No. of fertilized eggs/female[f]	0.00 ± 0.00a	280.19 ± 62.94b	313.07 ± 70.33b	267.39 ± 44.03b	318.50 ± 56.12b	6.3039	0.00041	10
Hatchability (%)[ef]	0.00 ± 0.00a	24.22 ± 3.48b	19.11 ± 2.28b	19.11 ± 2.20b	22.29 ± 3.87b	12.7305	< 0.0001	10

[a] Males: 20; females: 20; temperature: 25°C ± 1°C; RH: 60% ± 10%; 16L-8D: LED light only
[b] Mean ± standard error
[c] W: water (control); SW: sugar and water; PSW: pollen, sugar, and water; PHW: pollen, honey, and water; HW: honey and water
[d] Values for longevity indicate the number of individuals. Values for other life history parameters show the number of cages tested.
[e] Number of hatched clutches/total number of clutches
[f] Means with the same letters in the same row are not significantly different, and ns means not significantly different at the 5% level by the analysis of variance (ANOVA) and Tukey's honestly significant difference test.

Male BSF lived significantly longer than did females in all treatments. Adult longevity was the longest in the PSW treatment. Nakamura et al. (2016) also found that males live significantly longer than did females in the SW treatment.

The adult BSF consumes honeydew (Beuk 1990), which might be one of the main food sources in the field. We did not use honeydew or nectar as a food source, but honey might be a similar food source. Pollen is considered another essential resource for BSF, and in the wild, it might be the main source of protein, since pollen consists of 22.7% protein and 30.8% carbohydrates (Komosinska-Vassev et al. 2015). Bertinetti et al. (2019) suggested pollen as a possible food source in the wild populations of *H. illucens*, as in other Stratiomyidae (Oldroyd 1969). In terms of insect morphology, however, Rozkošný (1982) described them as nectar feeders having fully developed muscoid (spongelike)-type mouthparts, which was confirmed using scanning electron microscope images (Oliveira et al. 2016). We need to confirm the possibility of pollen as a food source. Feeding affects the longevity and egg production of the BSF (Bruno et al. 2019, Lupi et al. 2019, Nakamura et al. 2016).

Honey was another important source of energy for reproductive performance in our laboratory experiments. In many agroecosystems, pollen and honey offer greater dietary diversity than can be provided in laboratory rearing. In conclusion, the consumption of sugar and honey significantly increases longevity and reproductive success in BSFs. Accordingly, nectar, honeydew, and pollen are candidate natural food sources that will be confirmed by field studies.

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