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Black soldier fly larvae show a stronger preference for manure than for a mass-rearing diet

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Abstract

The attention for black soldier fly larvae (BSFL) as an alternative ingredient for food and feed products is on the rise. While many studies have reported the efficiency of BSFL to bio-convert a wide range of organic waste streams into larval biomass, so far, it is unknown whether BSFL prefer certain waste streams over others when they have the possibility to choose. Here, we performed a choice-test experiment to explore the preference of BSFL when exposed to pig manure and a mass-rearing diet consisting of plant by-products currently used for industrial BSFL production. We found that after 1 hr of exposure to both feeds, BSFL strongly preferred pig manure over the mass-rearing diet. The preference for manure became stronger as larval age increased. Our results provide the first evidence that BSFL express a distinct diet preference. Understanding the reasons for the strong preference for manure is relevant for a diverse array of practical applications and to inform the discussion on insect welfare.

KEYWORDS
behaviour, choice test, *Hermetia illucens*, manure, rearing

1 | INTRODUCTION

The mass-rearing of *Hermetia illucens* L. (Diptera: Stratiomyidae) larvae, hereafter called black soldier fly larvae (BSFL), is expanding worldwide. BSFL have become one of the main species for mass-rearing operations due to their ability to quickly convert a wide range of organic side streams into larval biomass that, if safe and allowed by law, can be used as an alternative source of food and feed. Together with the growth of industrial mass-rearing production, biological research on BSFL has also increased over the last years. Contemporary research topics include the determination of BSFL nutritional requirements (Barragan-Fonseca, Dicke, & van Loon, 2017), the estimation of feed efficiencies for different waste-stream diets (Lalander, Diener, Zurbrügg, & Vinnerås, 2019), the role of microbiota in growth and fitness of larvae and flies (De Smet, Wynants, Cos, & Van Campenhout, 2018), the exploration of environmental impacts associated with BSFL production (Smetana, Schmitt, & Mathys, 2019; Mertenat, Diener, Zurbrügg, 2019), food safety (Bosch, van der Fels-Klerx, de Rijk, & Oonincx, 2017; Lalander, Fidjeland, Diener, Eriksson, & Vinnerås, 2015) and mating and oviposition optimization in artificial conditions (Giunti, Campolo, Laudani, & Palmeri, 2018; Hoc, Noël, Carpentier, Francis, & Caparros Megido, 2019).

Although current research topics are diverse, a question that so far remained underexplored is: do BSFL prefer certain types of feeds over others? Usually, in both industrial and experimental conditions, BSFL are provided with only one type of feed, and therefore, it remains unknown whether BSFL prefer consuming certain feeds over others when they have the possibility to choose. Here, we performed a choice-test experiment in which larvae could choose between animal manure, a material in which BSFL naturally grow (Newton, Sheppard, Watson, Burtle, & Dove, 2005; Oliveira, Doelle, List, & O'reilly JR, 2015), and a mass-rearing diet consisting of plant by-products currently used for industrial BSFL production. The results reported here could be beneficial for the design of new feeding strategies and contribute to the discussion on insect welfare (van Huis, 2019) which is gaining interest.

2 | MATERIALS AND METHODS

2.1 | Larvae rearing

Seven-day-old BSFL (hereafter called starter larvae) that had been reared on a mix of wheat bran and water at the facilities of Bestico B.V, the Netherlands, were packed and shipped to the facilities of Wageningen University & Research, where the choice test was conducted. A group of starter larvae was separated to perform the first choice test (see Section 2.3), whereas the rest of the starters were reared in two independent crates, one containing fresh pig manure and the other containing the mass-rearing diet. These two diets were provided to the starters to assess a potential effect of larval diet on preference behaviour. In each crate, 5 kg of either pig manure or the mass-rearing diet was added together with 5,000 starter larvae (for details on the feeds, see Section 2.2). Both crates were located in a climate-control room at 27°C, 70% relative humidity and a 12-hr light–dark cycle. At ages 9, 12, 14 and 16 days, 10 groups of 50 larvae each were collected randomly from the pig manure crate and from the crate containing the mass-rearing diet. The groups of 50 larvae were used as replicates to perform the choice tests (see Figure 1).

2.2 | Feeds

The fresh pig manure, collected on the first day of the experiment, had a dry matter content of 24.1%. The manure was produced by 20-week-old sows of the breed Topigs 20 fed with the feed "Uniek Start," from AgruniekRijnvallei, Wageningen, the Netherlands. The mass-rearing diet used by Bestico B.V. was shipped on the first day of the experiment and had a dry matter content of 28.6% dry matter. The feed was composed of a mixture of three commercial products: ProtiWanze® (by-product from bioethanol production from wheat starch, which contains wheat protein, sugar beet syrup and yeast), DB-blend (made of wheat starch and potato leftovers) and a binding agent. The proportion of each ingredient (fresh matter basis) was ProtiWanze 47%, DB-Blend 47% and binding agent 6%. Both feeds were stored in a refrigerator at 5°C upon arrival. On every choice-test day, refrigerated samples of both feeds were collected to perform the choice test. These samples were allowed to reach room temperature (27°C) before the start of the choice tests.

2.3 | Choice test

For the choice test, two diagonally opposite corners of a cubic rounded-corner plastic container (20 cm × 20 cm × 20 cm) were filled each with a full 15-ml spoon of pig manure whereas the other two diagonally opposite corners were filled each with a 15-ml spoon of the mass-rearing diet (Figure 1a). Subsequently, a group of 50 larvae (which were randomly collected from each crate as indicated in Section 2.1) was placed in the middle of the plastic container and left for one hour in a climate-control room at 27°C and 70% relative humidity under complete darkness. Plastic lids were placed on top of each container to prevent escapes. After one hour, the container was removed from the climate-control room, and straightaway, each of the four piles of feed was collected in separated flasks for counting of larvae using water and sieves of different mesh sizes (0.25–3 mm). If larvae were found outside the piles (i.e. in the middle

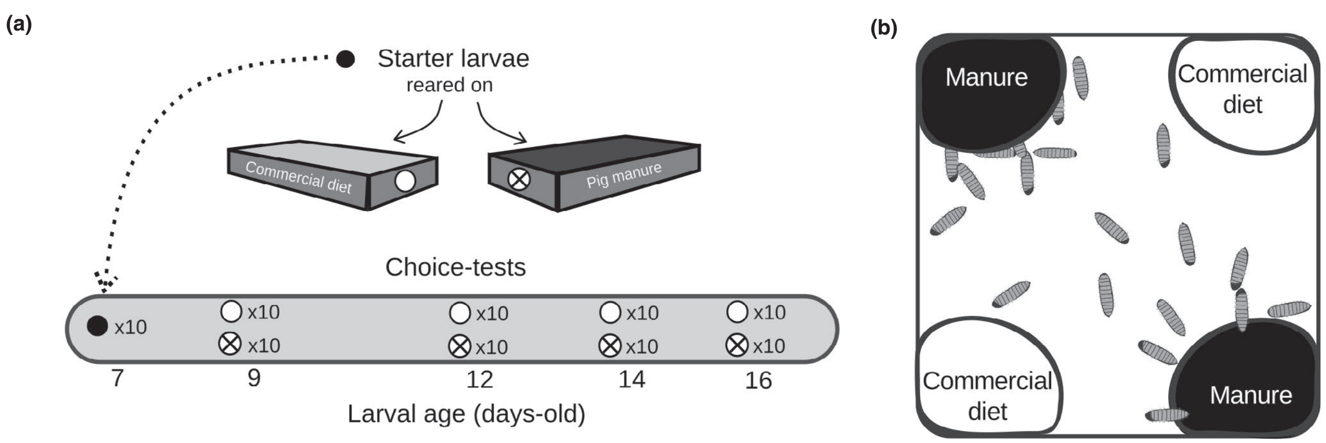

FIGURE 1 (a) Experimental design. Circles represent a group of 50 larvae. The black circle represents starter larvae, the white circle represents larvae reared on mass-rearing diet, and the crossed circle represents larvae reared on pig manure. Every choice test was replicated 10 times. (b) Schematic representation of the test arena

of the container, climbing the walls of the container or between piles), these were scored as "no choice." Larvae were removed from the experiment after the quantification of the number of larvae in each pile. Ten replicates were done for each choice test.

Exploratory videos were recorded at different larval ages to the purpose of visual illustration of BSFL behaviour in our test arena (see Video S1 and Figure S1 for details). Choice test that was recorded was not considered as replicates and therefore was not included in our results.

2.4 | Statistical analysis

Repeated *G* tests were performed to test whether there was an overall deviation from an equal proportion of larvae found in manure and the mass-rearing diet for each larval age. For each replicate, the numbers of larvae found in both manure piles were summed and the numbers found in both mass-rearing diet piles were also summed. In addition, log-linear regression models were performed to assess the effect of the following parameters: larval age (i.e. 7, 9, 12, 14 and 16 days old), initial diet (i.e. mass-rearing diet or manure) and replication (i.e. from 1 to 10), on the degree of preference of the larvae for manure or the mass-rearing diet.

3 | RESULTS

In all replicates, most of the larvae were found in the piles of pig manure, and only a few or sometimes not a single larva was found in the piles with the mass-rearing diet (Figure 2, Table S1). The video

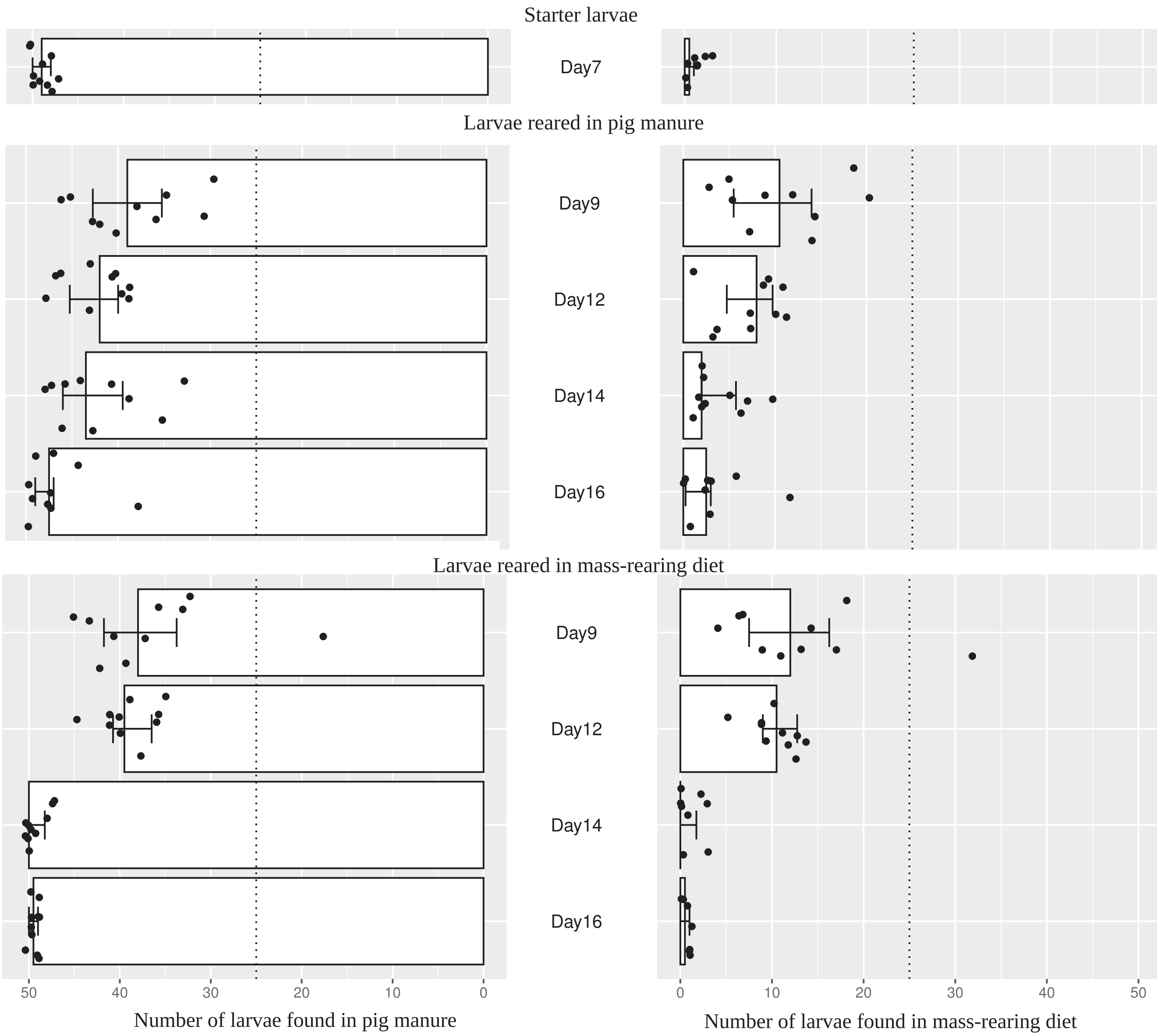

FIGURE 2 Summarized results of the choice test. Bars show the median value of the 10 replicates, and error bars show the 25% and 75% quartiles. It should be noticed that in case of an equal distribution of larvae between the mass-rearing diet and manure, both bars should be close to the dashed line, which marks the values for an equal distribution of 25 larvae in both substrates

records, however, confirmed that during the choice test BSFL moved actively within the container and tried both feeds (see Video S1). The proportion of larvae scored as "no choice" was negligible (Table S1), with the exception of day 14 for the larvae growing on manure, in which for some replicates, groups of larvae ranging from 5 to 10 individuals were found climbing the walls of the containers.

The preference of BSFL for manure over the mass-rearing diet was observed at all ages and regardless of whether the larvae were previously fed with pig manure or with the mass-rearing diet (Table 1). However, the preference for manure became stronger as larval age increased (estimate = 0.04, $z = 5.54$, $p < .0001$). Although larvae were found in both piles of manure (see Table S1), these tended to aggregate in one pile rather than being equally distributed in both piles (estimate = −0.08, $z = -2.49$, $p = .01$). Lastly, the type of diet to which the larvae were exposed prior to the preference test did not have any effect on the observed preference (see Table S2).

4 | DISCUSSION

The results of the choice tests demonstrate that BSFL strongly prefer pig manure over a mass-rearing diet, regardless of their age and the type of feed the larvae were reared on. While it was not the aim of this research to elucidate the underlying factors driving the preference of BSFL for manure, here we discuss three potential factors that could have influenced the observed preference: microbial diversity of the substrate, pH and chemosensory cues.

While pH is an important factor influencing the microbial community of a medium (Zhang, Qiu, & Chen, 2012), the microbial diversity of the substrate in which BSFL grow is a key factor for larval development. Microbes not only directly affect the capacity of the larval gut to digest certain compounds (Bruno et al., 2019; Gold, Tomberlin, Diener, Zurbrügg, & Mathys, 2018), but those present in the substrate, if beneficial for the larvae, can supply bacterial-digested compounds that help to achieve higher bioconversion efficiencies in BSFL bioconversion systems (Jiang et al., 2019; Rehman, Cai, et al., 2017; Rehman, Rehman, et al., 2017; Xiao et al., 2018; Yu et al., 2011). Considering that the bacterial loads, richness and diversity in the mass-rearing diet were lower compared to chicken manure (Wynants et al., 2019), it is likely that these were also lower compared to pig manure. Future research efforts should focus on elucidating if BSFL are attracted to feeds with higher bacterial loads and/or higher bacterial diversity and if this attraction is related to the presence and abundance of bacterial-digested compounds. If BSFL larvae are attracted due to higher microbe-produced compounds, the observed preference would likely be a result of an attraction to manure rather than a disgust to the mass-rearing diet.

Besides the microbial diversity of the substrate, the pH of the substrate is another factor that needs to be explored for its potential to affect BSFL choices. While the pH of fresh pig manure used in the experiment ranged between 6 and 7, the pH of the mass-rearing diet feed ranged between 3 and 4 (this pH is intentionally used to stabilize the feed in the storage tanks). Even though BSFL are able to survive and grow on diets with a wide range of pH (pH 4–9.5) (Ma et al., 2018; Meneguz, Gasco, & Tomberlin, 2018), it has been found that in a batch feeding system, BSFL grew heavier on slightly acidic (pH 6) or slightly basic conditions (pH 8–10). The exploratory video records confirmed that during the choice test BSFL moved actively within the container and tried both feeds (Video S1). After 1 hr, however, most larvae were found in the pig manure (Table 1). Hence, more research is needed to (a) understand whether BSFL choices are sensitive to pH differences in feeds but without the influence of confounding variables (e.g. feed type, moisture levels, microbial loads) and (b) whether the response to pH is mediated by disgust to acid substrates as this could have implications for insect welfare.

Finally, even though there are no studies on chemosensory cues for BSFL, research on other fly species shows that flies in both larval and adult stages are able to recognize different substances. *Drosophila* larvae, feeding on yeasts on rotting fruit substrates, for instance, are able to detect fruit compounds through 90% of its olfactory receptors (Dweck et al., 2018). Specific compounds isolated from fermented wheat bran were found to cause a

TABLE 1 Total number of larvae that preferred the mass-rearing diet and pig manure. Total *G*-values and *p* values were calculated using repeated G tests of goodness of fit. The abbreviation *df* refers to degrees of freedom

Reared on	Age (days)	Preferred: Manure	Preferred: Mass-rearing diet	No choice	Total *G*	*df*	*p* value
Any	7	489	8	3	620.1262	10	8.56E-127
Manure	9	386	108	6	203.9185	10	2.46E-38
Manure	12	426	72	2	299.7459	10	1.76E-58
Manure	14	422	39	39	393.2478	10	2.57E-78
Manure	16	469	30	1	505.2718	10	3.30E-102
Mass-rearing diet	9	366	131	3	173.3952	10	5.49E-32
Mass-rearing diet	12	391	105	4	184.2149	10	3.12E-34
Mass-rearing diet	14	491	9	0	621.1553	10	5.15E-127
Mass-rearing diet	16	495	5	0	644.1276	10	6.12E-132

physiological response in adult housefly antennae and to increase both substrate attractiveness and oviposition (Tang et al., 2016). Thus, considering that adult BSF flies naturally lay eggs in decomposing material, including animal manures (Newton et al., 2005; Oliveira et al., 2015), and that pig manure emits a variety of volatiles (Schiffman, Bennett, & Raymer, 2001), future research should focus on finding if olfactory receptors in both BSFL and adult flies are stimulated when exposed to animal manures or any other decomposing material, and how olfactory receptor activation patterns relate to attraction.

Even though we evaluated the preference over a short period of time (1 hr) and it cannot be excluded that the larvae will switch between diets over a longer period as a mechanism to balance the intake of different nutrients (Rho & Lee, 2014; Simpson & Raubenheimer, 2012), the mechanisms behind the initial strong preference for manure reported here could be of particular interest to the insect industry and related stakeholders. On the one hand, if the preference is mainly caused by specific compounds in the manure to which the larvae are attracted, these compounds could be used for a diverse array of practical applications, including the design of alternative feeding strategies, the prevention of larval escapes from rearing crates and the establishment of alternative methods for harvesting larvae. On the other hand, if the preference for manure is predominantly driven by the physical (e.g. moisture, texture) and/or biochemical (e.g. pH) properties of the medium, these conditions, when possible, could be either mimicked if they increase preference or avoided in case they cause avoidance enabling producers to make their diets more appropriate for BSFL development. The latter is relevant for the emerging discussion on insect welfare. While it is still uncertain if insects are sentient beings (organisms that feel, perceive and experience subjectively) (see discussion in van Huis, 2019), the International Platform of Insects for Food and Feed (IPIFF) has adopted the precautionary principle and has called upon all insect producers to implement high standards of animal welfare and care to promote insect well-being (IPIFF, 2019). Our results give a first indication that BSFL have a feed preference. Research efforts are needed to evaluate whether discomfort, distress and the freedom to express normal behaviour are factors that drive the observed preference and whether they are related to animal welfare and productivity.

In all cases, before any implementation is done, potential trade-offs with food safety (i.e. increasing pH could foster the proliferation of pathogen bacteria in storage tanks), environment (i.e. increasing the pH could lead to higher ammonia emissions) and production costs should be first assessed to avoid undesirable consequences.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

AP conceived the idea and wrote the paper. AP and JJAVL designed the research. AP and KVD conducted the experiments and analysed the data. IJMDB secured funding. JVS contributed material. JJAVL, IJMDB, JVS and HHEVZ critically revised the manuscript and contributed to its final version.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are presented in the paper and its supporting information. The supporting information (Video S1, Figure S1, Table S1, Table S2) and R codes for analysis and visualizations are available in the following repository: https://doi.org/10.4121/uuid:087b8581-71b6-4bac-914b-1807ebcf90b4.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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