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Impact of Male and Female Body Size on Mating Performance and Reproductive Success in Black Soldier Fly, *Hermetia illucens* L. (Diptera: Stratiomyidae)

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ABSTRACT

Mating and Reproductive success is the most essential phase in establishing efficient maintenance to ensure a sustained supply of Black Soldier Fly/BSF populations. This study aims to ascertain the influence of mating partner body size on successful mating and reproduction in BSF. Adult males and females BSF of the same age (< 24 hours) were paired based on a combination of body size treatments (large, average, small). Semi-outdoor observations were conducted in 30x30x30 cm nylon net cages, with each treatment repeated three times. The observation parameters include mating frequency, oviposition frequency, egg number, egg weight, and egg viability or fertility. The differences in body size of mating partners significantly influence mating and reproductive success in BSF. The combination of a mating pair consisting of a large male and a large female had the highest frequency of mating (35.3 ± 4.64) and oviposition (28 ± 2.04), whereas mating pairs of a small male and a small female had a low mating frequency (13.7 ± 5.18) and lowest oviposition (5.0 ± 0.63). Mating tended to occur more frequently when males were matched with large females than when males were paired with average or small females.

Keywords: black soldier fly, body size, mating success, reproductive potential.

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INTRODUCTION

The Black Soldier Fly (BSF), *Hermetia illucens* (Linneus 1758) is a significant non-pest insect that has gained a lot of interest, particularly because of its potential to transform organic wastes into prepupal biomass as a renewable resource with great economic value. The success of mating and reproduction significantly impacts the availability of BSF populations (Liu, Lang, Hao, Hu, & Li, 2023; Julita, Fitri, Putra, & Permana, 2020; Hoc, Noel, Carpentier, Francis, & Megido, 2019). In many insect species, body size is also the main determinant of mating success. Body size, particularly in males, is regarded as a key factor influencing mating success in a variety of insect species (Jones & Tomberlin, 2021). Recent studies have highlighted the significance of body size in influencing the reproductive success of *Hermetia illucens*. Renault, Aubin-Horth, & Saucier (2023) investigated the effects of phenotyping, adult selection, and mating strategies on the reproductive outcomes of *H. illucens*. Their findings suggest that selecting individuals based on specific phenotypic traits, including body size, can enhance reproductive efficiency. Larger individuals, particularly males, exhibited higher mating success and contributed to increased oviposition rates in females. Additionally, research by Zaalberg, Smith, & Doe (2024) explored mating strategies in *H. illucens*, specifically investigating the feasibility of controlled and polygynous mating systems. The study demonstrated that males are capable of mating with multiple females, and such controlled mating approaches can be effectively implemented. This strategy not only facilitates efficient pedigree-based breeding programs but also allows for the selection of desirable traits, including optimal body size, thereby potentially enhancing reproductive success and overall fitness in black soldier fly populations. Male and female sexual selection mechanisms significantly impact mating and reproductive success in insects. Mating pairs use sexual selection to obtain beneficial investments for their offspring's survival (Hunt, Roux, Wood, & Gilburn, 2002; Armitage, 1995). Females' mating strategy will consider males with good genetic traits (good gene hypothesis). Physical traits of males can be used to predict the quality of the reproductive system, such as sperm quality and the survival rate of males as potential mating partners. Female preferences for male physical traits are associated with reproductive success and the quality of offspring produced (Nguyen, 2015). Adult male and female quality can be expressed by physical traits such as body size, body weight, and the appearance of attractive body ornamentation (Tanner, Garbe, & Zuk, 2019; Nguyen, 2015; Blaul & Ruther, 2012; Xu, 2010; Miller & Pitnick, 2002; Blanckenhorn, Muhlhauser, Morf, Reusch, & Reuter, 2000).

During mating, however, black soldier flies (BSF) may experience sexual conflict (Giunti, Campolo, Laudani, & Palmeri, 2018). As they try to copulate, males are known to swiftly beat their wings and tap the female abdomen with their tarsi. Male size may be related to the frequency, duration, and success of wing-beating (Jones & Tomberlin, 2021). BSF females with larger wing sizes and body sizes have higher fertility rates compared to females with smaller wing and body sizes (Gobbi, Martinez-Sanchez, & Rojo, 2013). Adult insects rely on nutrients collected during the larval stage. The relationship between larval competition and reproductive success in insects that feed as adults has been intensively studied (Hooper, Spagopoulou, Wylde, Maklakov, &

Bonduriansky, 2017; Fricke, Adler, Brooks, & Bonduriansky, 2015). Adult BSF appears to rely on larval energy stores to aggregate, secure mates, and produce offspring (Sheppard, Tomberlin, Joyce, Kiser, & Sumner, 2002). Adult BSF do not require food and simply require water to survive (Tomberlin, Sheppard, & Joyce, 2002). A lot of research has investigated the effect of different feeding rates on the development period and body size of various black soldier fly larvae densities (Barragan-Fonseca, Dicke, & Van Loon, 2018; Myers, Tomberlin, Lambert, & David, 2008; Parra Paz, Carrejo, & Gómez Rodríguez, 2015). Many studies found that high larval densities with restricted food resources resulted in smaller larvae and prepupae when compared to experimental methods with low density and optimal food supply.

Males from low larval densities have larger body sizes, higher and faster mating success, and mate more frequently than smaller males from higher larval densities (Turiegano, Monedero, Pita, Torroja, & Canal, 2013; Wigby, Perry, Kim, & Sirot, 2015). Females originating from the medium with low larval density have a larger body size, achieve higher mating success, and remate more quickly than smaller females emerging from high larval density treatment (Amitin & Pitnick, 2007; Wigby, Perry, Kim, & Sirot, 2015). Although research on the economic importance and application of BSF's ability to convert various organic wastes into biomass high in protein and fat has been widely published, reports on basic biological aspects related to body size mating partner that influence mating behavior and reproductive success of BSF are still very limited and have not been widely explored. Reproduction is the most crucial phase in developing efficient maintenance of BSF to create sustainable BSF population availability (Julita et al, 2020; Hoc et al, 2019).

This study aims to investigate sexual selection in BSF depending on the body size of mating partners and its impact on mating success, fecundity, and fertility of eggs. This information is essential and can be applied to develop an efficient BSF maintenance system that ensures optimal and sustainable availability of the BSF population.

MATERIALS AND METHODS

Study site

This study was carried out at the integrated garden of the Faculty of Science and Technology at UIN Sunan Gunung Djati in Bandung. For 4 months, all observations of sexual selection behavior depending on the body size of BSF mating partners were conducted semi-outdoors in a screen house of 5 x 5 x 4 m^3.

Procedures

BSF eggs were obtained from adult BSF colonies maintained at the Toxicology Laboratory, School of Life Sciences and Technology, Bandung Institute of Technology. Egg colonies were placed in plastic trays (30 x 25 x 10 cm) containing chicken feed with 60% humidity as a medium for egg hatching. The hatched larvae were reared in three treatments with different feeding rates to obtain the BSF adult body size groups (large, average, small) needed for the experiment. The chicken feed used as a larval growth medium contained 150 mg/larva/day (large group), 100 mg/larva/day (average group), and 50 mg/larva/day (small group). The prepupa is maintained until reaches the pupal stage which is characterized by an immobile, stiff, and dry body. The size of the pupa correlates with the size of the adult when it emerges from the pupa. Subsequently, pupae were selected and categorized based on homogeneous body size for use in the experiment. The size classification included small (length: <17.01 mm; weight: <0.083 g), average (length: 17.01-20.06 mm; weight: 0.083-0.118 g), and large (length: >20.06 mm; weight: >0.119 g).

To verify that the individuals used in the experiment were the same adult age and to ensure the virginity of males and females, the pupae were maintained individually in plastic cups and then covered with black cloth. A total of 1080 male and female adult BSFs of the same age (under 24 hours) were paired up using a combination of body size (Table 1). The treatment of mating partner body size variations on mating success and reproduction was carried out entirely semi-outdoor in nylon net cages measuring 30x30x30 cm installed in a screen house with three replications. Each cage has a drinking water source and an ovitrap (three layers of wood, each with a length of 15 cm and a width of 5 cm) placed on a decomposing organic substrate to attract female oviposition and collect BSF eggs.

Body size combinations	
Males	Females
Small	Small
Small	Average
Small	Large
Average	Small
Average	Average
Average	Large
Large	Small
Large	Average
Large	Large

Table 1. Body size combinations of BSF mating pairs treatment.

Mating observations were conducted daily over a 14-day period to systematically document mating behaviors in *Hermetia illucens*. Observations were performed at 20-minute intervals within 1-hour time blocks throughout the daylight period, from 06:00 to 18:00 hours. This observation schedule was designed to capture temporal variations in mating activity while minimizing potential observer bias. The selected time frame aligns with the known diurnal mating patterns of *H. illucens*, particularly in the morning and late afternoon. The 20 minute observation intervals within each hour ensured sufficient temporal resolution to detect changes in mating behavior while maintaining feasibility for long-term monitoring. This study’s observation parameters are (1) total mating frequency, (2) daily mating frequency, (3) total oviposition frequency, (4) daily oviposition frequency, (5) number of eggs, (6) egg weight, and (7) viability or egg fertility (the number of eggs that hatch into larvae). The number of females laying eggs on the ovitrap was used to determine the frequency of oviposition. The number of eggs found in the ovitrap is used to calculate the daily number of eggs.

This study was conducted in a semi-outdoor environment, where environmental parameters were recorded through direct measurements throughout the 14-day observation period. Temperature, humidity, and light intensity were continuously monitored in real-time to assess their potential influence on mating performance. The observed temperature averaged 28.1°C, with fluctuations between a minimum of 24.0°C and a maximum of 31.6°C. Relative humidity was recorded at an average of 81%, ranging from 74% to 87%. Meanwhile, light intensity varied between 7,622.12 and 12,272.39 lux, with a mean value of 9,882.14 lux.

Statistical analysis

Statistical analysis of variance (ANOVA) with Duncan's post hoc test was used with a 95% confidence level or $\alpha = 0.05$ as the significance level (Kim et al., 2010) to assess differences between treatments in the parameters of total mating frequency, oviposition frequency, number of eggs, egg weight, and egg fertility. SPSS 25.0 software was used for all statistical analyses.

RESULTS AND DISCUSSION

Mating frequency of Black Soldier Fly

The combination of body size of male and female mating partners (as shown in Fig. 1) significantly influences ($P<0.05$) the total mating frequency in BSF. The highest average total mating frequency (35 pairs) was found in mating pairs of large males and large females. Among the other treatments, the body size treatment of mating pairs consisting of small males and small females had the lowest mating frequency (Fig. 2). The combination of body size treatments for other mating partners resulted in varied mating rates, with males partnered with large females having a higher mating frequency than males paired with average or small females. The body size of the mating pair influences mating success in BSF. This is consistent with previous studies, which found that mating success improved by 50 to 100% in BSF mating pairs with varying combinations, such as large males and small females or small males and large females (Jones & Tomberlin, 2021).

Figure 1. The combination of body size of male and female mating partners, a) small female and large male; b) large female and large male.

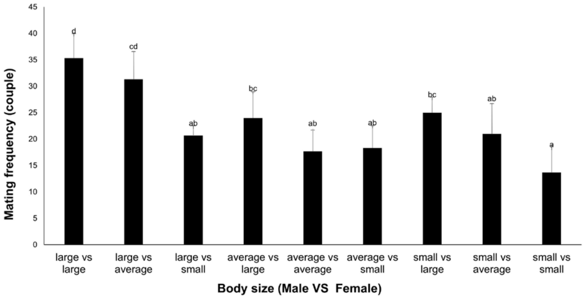

Figure 2. Total mating frequency of BSF in the treatment of differences in body size of mating partners (different letter bars indicate statistically significant differences, α= 0.05).

Large males are generally twice as aggressive as little males. In the mating behavior of the black soldier fly (*Hermetia illucens*), aggressiveness is primarily observed in male competition for mates. More aggressive males exhibit higher levels of aerial competition, frequent chasing, and increased physical interactions such as mid-air collisions to establish dominance over other males (Tomberlin & Sheppard, 2001). These behaviors are particularly prominent in larger males, which tend to defend prime mating locations more vigorously (Jones & Tomberlin, 2021). Less aggressive (or smaller) males display fewer competitive interactions and may adopt alternative strategies such as waiting on the periphery for mating opportunities (Julita et al., 2020).

The impact of male and female body size differences on mating success has been reported in various species of insects. Large males exhibited a higher number of mating successes than small males in *Bactrocera tryoni* (Diptera: Tephritidae) (Ekanayake, Clarke, & Schutze, 2017) and *Cotesia urabae* (Hymenoptera: Braconidae) (Avila, Withers, & Holwell, 2017). Females prefer large males, according to observations of the swarming behavior of male *Anopheles freeborni* (Diptera: Culicidae) in their natural environment (Yuval, Wekesa, & Washino, 1993).

On the second day of observation, all mating pair combination treatments began to demonstrate mating activity and successful copulation, with the highest number of mating pairs on the second and third days of observation. The pattern of mating frequency varied across treatments but tended to decrease until the end of the mating period, except for large male and large female mating partners, which experienced an increase in mating frequency on the fifth day of observation. The body size treatment of large males and large females, as well as large males and average females, had the longest mating period, with mating pairs still detected that copulated successfully until the seventh day of observation.

Mating pairs of large males and small females, as well as small males and small females, had the shortest mating period, lasting only two days, with mating success seen only on the second and third days of observation (Fig. 3). A longer mating period promotes remating activity in BSF, allowing it to produce more eggs (Julita et al, 2020). According to previous studies, adult BSF began mating activities on the second day after emerging from the pupa, in the morning when the weather was sunny and beginning to warm. Mating activity peaks between 11:00 and 12:00 a.m. when the daily sunlight intensity reaches its peak. Adult BSF is strongly dependent on daylight for initiating mating activities, and optimal sunlight is required to identify the presence of female mating partners (Julita et al, 2020; Zhang et al, 2010; Holmes, Vanlaerhoven, & Tomberlin, 2012).

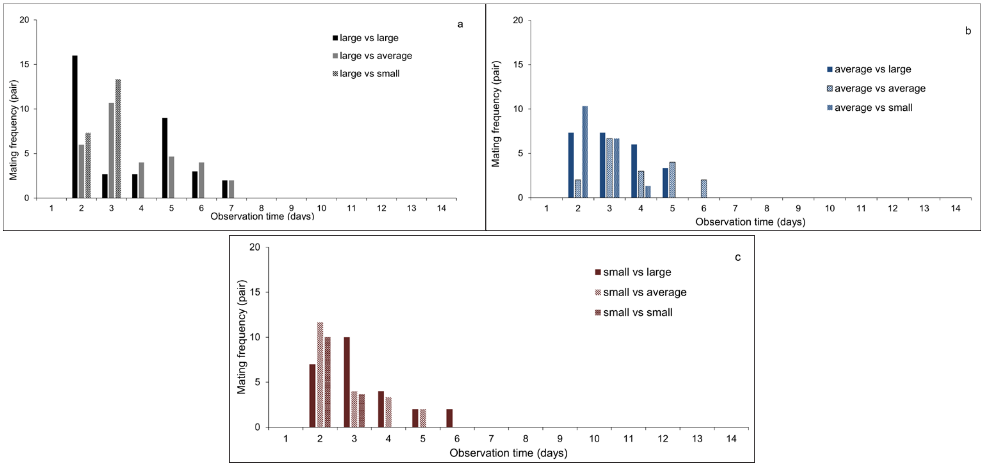

Figure 3. The daily mating frequency of BSF under different body size treatments of mating pairs: a) large male mating pairs, b) average male mating pairs, c) small male mating pairs.

In the combination treatment of male and female body size, the average mating duration or length of BSF copulation time was between 21 and 35 minutes. The combined treatment of small males and large females had the longest mating duration, whereas mating pairs of average males and small females had the shortest (Fig. 4).

Figure 4. Mating duration of BSF in all body size treatments (same letter bars indicate statistically not significant differences (α = 0.05).

The duration of mating can be related to the amount of sperm transfer delivered by the male to the female. Sperm transfer rises as the time of copulation increases. Mating duration also provides males with an advantage over competitors in terms of the number of sperm they possess (Xu, 2010). However, there was no statistically significant difference in mating duration between the combination of mating partner body size in this study.

Oviposition frequency

The frequency of oviposition represents the number of females that successfully lay eggs. This oviposition frequency data corresponds to the mating frequency data in Fig. 2.

The highest frequency of oviposition was found in the treatment of large males and large females (28 individuals), large males and average females (27 individuals), and males paired with large females, specifically small males with large females (17 individuals) and average males with large females (15 individuals) (Fig. 5). Males partnered with small females had the lowest daily oviposition frequency. Mating pairs of large males and small females were observed to lay eggs only once during the oviposition period, on the seventh day, or at the end of the oviposition period. Large female insects have larger ovaries and are more sexually developed than smaller females. Large females have a higher fertility rate, thus males prefer large females, and large females attract mating partners more quickly (Aluja, Rull, Sivinski, Trujillo, & Pérez-Staples, 2009).

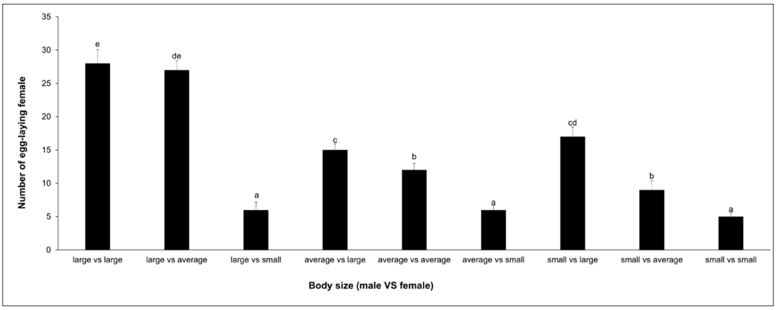

Figure 5. Oviposition frequency of BSF females with differences in body size of mating partners (different letters bars indicate statistically significant differences (α = 0.05)).

Total number of eggs, total weights of eggs, and egg fertility

According to the statistical analysis, there were significant differences in egg number and egg weight between treatments. The combination of large male and large female body size generated the most total eggs (8125 eggs), followed by the large male and average female treatment (7908 eggs). The average egg weight correlates to the average number of eggs produced across all treatments. When partnered with small females, males of all sizes produced the fewest eggs on average (Fig. 6).

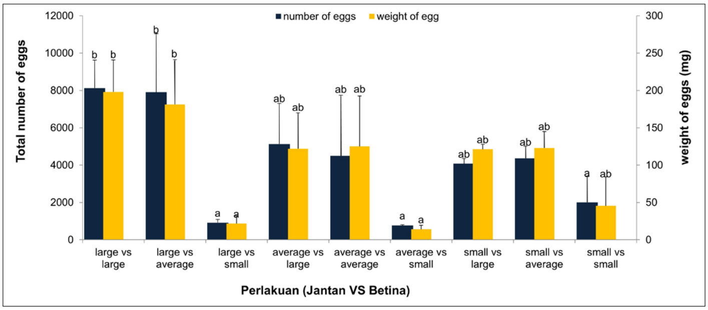

Figure 6. The number of eggs and egg weight obtained in each treatment combined body size (different letters bars indicate statistically significant differences (α = 0.05)).

Female fecundity in other insects correlates to body size (Calvo & Molina, 2005; Klingenberg & Spence, 1997; Honek, 1993). The quantity of eggs is related to the adult female body size. Larger BSF females are more fertile and will lay more eggs than small females (Gobbi et al., 2013; Wardhana, 2016). Larger BSF females can generate 50% more eggs than smaller females (Jones & Tomberlin, 2021). The adult female's size reflects her ability to produce eggs. This association has been observed in a variety of different insects (Morimoto, Nguyen, Tabrizi, Ponton, & Taylor, 2018; Calvo & Molina, 2005). In *Aedes aegypti* (L.) (Diptera: Culicidae), larger females generated 50% more eggs than smaller females. The quantity of viable eggs produced by large and small females varies depending on whether they mate with large or small males (Dieng et al, 2016).

Mating and reproductive success are determined by the quantity of viable eggs generated in subsequent offspring. Egg fertility indicates the amount of eggs that successfully hatch into larvae or viable eggs. Fig. 7 shows fertility rates in mating pairs with different male and female sizes. The egg fertility value in this study ranged from 71.33% to 90.3%. The highest fertility was found in males of all body sizes paired with small females. Fertility refers to the capacity of sperm cells to fertilize egg cells. Fertile eggs are eggs that are successfully fertilized by sperm and can hatch into offspring. Egg fertility in insects is correlated with the number of sperm stored in the spermatheca of female insects. The body size of the male mating partner in insects is positively correlated with the total number of fertile eggs laid by the female (Blay & Yuval, 1999). In another insect, *Ephestia kuehniella*, females with larger body sizes have high fecundity, while males with larger body sizes will produce larger spermatophores thus they can increase the fertility of the eggs produced by the female. Larger females are preferred for remating with previous or new mating partners (Xu, 2010).

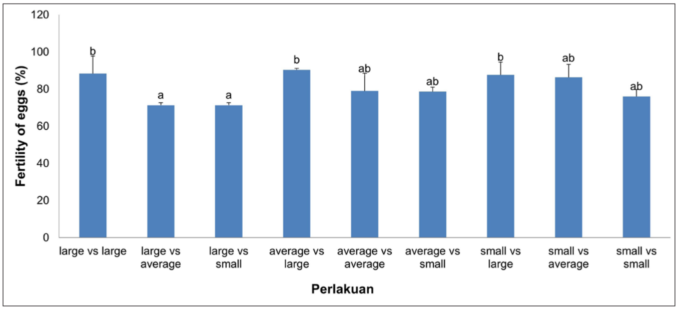

Figure 7. Fertility or egg viability in each combined mating pair (different letter bars indicate statistically significant differences (α = 0.05)).

In insects, the large body size of the male indicates that the male has good qualities. Large males have better genes and a larger ejaculate supply than small males. In some insect species, males that have a larger body size have a higher chance of obtaining a mating partner and may mate more frequently. Meanwhile, in females, body size influences egg supply, larger females produce more eggs compared to smaller females (Xu, 2010). Thus, mating pairs involving large males and females will have better mating and high reproductive success compared to mating pairs without large mating partners.

The findings of this study provide valuable insights into the role of body size in mating success and reproductive performance in BSF, which can be directly applied to the optimization of breeding programs. The observed higher mating and oviposition frequencies in pairs consisting of large males and large females suggest that selecting for larger individuals in breeding colonies could enhance overall reproductive efficiency. Furthermore, the increased egg fertility associated with large females, regardless of male body size, indicates that prioritizing the rearing and selection of larger females may be a key strategy for maximizing egg production. These insights can inform selective breeding approaches aimed at improving BSF population sustainability and productivity, ultimately contributing to large-scale BSF rearing for waste bioconversion and sustainable protein production. Additionally, understanding size-dependent reproductive success can help refine mating management practices, such as optimizing stocking densities and environmental conditions to promote ideal mating pair formations, further enhancing breeding outcomes in commercial and research settings.

CONCLUSION

The body size of male and female mating pairs plays a crucial role in determining mating success and reproductive output in BSF. Mating pairs consisting of a large male and a large female exhibited the highest overall mating and oviposition frequencies among all body size combinations. Additionally, males of all sizes (large, average, and small) that mated with large females demonstrated higher mating and oviposition success, along with greater egg fertility. A pairing between a large male and a large female resulted in the highest egg production, highlighting the significance of body size in reproductive efficiency. These findings have broader implications for commercial BSF breeding programs, particularly in optimizing selective breeding strategies to enhance colony productivity. The results suggest that prioritizing larger individuals in breeding stock could improve reproductive efficiency and overall egg yield, benefiting large-scale BSF farming for waste bioconversion and sustainable protein production. Additionally, future studies should explore other influencing factors such as environmental conditions, nutritional inputs, and genetic diversity to gain a more comprehensive understanding of reproductive success in BSF. Investigating these variables could further refine breeding protocols and contribute to the development of more efficient and resilient BSF production systems.

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