Selected Life-History Traits of Black Soldier Flies (Diptera: Stratiomyidae) Reared on Three Artificial Diets

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ABSTRACT *Hermetia illucens* (L.) was reared on three larval diets to determine their effects on preimaginal development and selected adult life-history traits. Prepupal and adult characteristics were examined for individuals reared on each diet and compared with field-collected prepupae and corresponding emergent adults. Diet did not significantly influence development or survivorship to the prepupal stage. However, adult emergence for all diets was significantly less than that determined for the wild population. Development time from egg to adult for individuals reared on the diets at 27°C ranged from 40 to 43 d with the larval stage lasting 22–24 d. We observed >96% larval survivorship to the prepupal stage and 21–27% adult emergence. Females accounted for 55–60% of emergent adults across treatments. Specimens reared on each diet were reduced in size, longevity, and calorie content in comparison to specimens from the wild population. Males within diet treatments and field-collected specimens were significantly smaller than females and emerged 1–2 d before females. Additionally, males reared on the diets and provided water lived for 9 d, whereas females lived for 8 d. This information indicates the diets might be used for rearing soldier flies. However, further refinement is needed to produce adults similar to those found in nature.

KEY WORDS Diptera, Stratiomyidae, *Hermetia illucens*

THE BLACK SOLDIER FLY, *Hermetia illucens* (L.), is a large (13 to 20 mm), wasp-like fly (May 1961). It has three generations per year in the southeastern United States and can be collected from late spring through early fall (Sheppard et al. 1994). Larvae occur in assorted decomposing materials, such as fruits, animals, and manure (James 1935).

The black soldier fly is interesting because its presence can be used to solve many of the problems associated with large manure accumulations at confined animal feeding operations. House fly, *Musca domestica* L., control due to manure being colonized by the black soldier fly has been reported by Furman et al. (1959), Tingle et al. (1975), Sheppard (1983), and Axtell and Arends (1990). Additionally, Tingle et al. (1975) documented that black soldier fly larvae reduce waste within poultry facilities. Sheppard et al. (1994) followed up their work and determined that the black soldier fly can reduce manure accumulation by 42–56%. Concentrations of nitrogen, and other nutrients are also significantly lower in this reduced manure (D.C.S. unpublished data), thus further reducing the potential for pollution.

Soldier fly prepupae can be used as feed for a variety of animals, including fish (Bondari and Sheppard 1981) and swine (Newton et al. 1977). Prepupae, when dried, have an estimated value comparable to menhaden fish meal. If used live, as specialty feed, or marketed to exploit its other unique qualities (i.e., essential fatty acids and chitin), the value of the product might be higher (Sheppard et al. 1994). Additionally, a system has already been developed for self-harvesting the larvae by directing their search for pupation sites into collection bins (Sheppard et al. 1994).

This manure management system depends on a robust soldier fly population for dependable inoculation of the manure with larvae. Presently, little is known about the biology of *H. illucens.* Rearing of the black soldier fly has been attempted in the past (Tingle et al. 1975) but was unsuccessful until 2002 (Sheppard et al. 2002). With the development of suitable methods, the soldier fly can now be produced and made available as a biological control and waste management agent.

The primary objective of this study was to determine basic biological parameters for the black soldier fly when reared in selected diets. Additionally, we compared life-history data for prepupae and adults reared in these diets to data recorded for field-collected prepupae and the emergent adults. Information from this study is important for improving rearing methods necessary for integrating the black soldier fly into current waste management strategies in livestock and poultry facilities.

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Table 1. Composition (%) of diets used to rear black soldier flies

Constituent	Gainesville diet	CSMA	Layer hen ration
Alfalfa meal	30.0	27.0	[a]
Wheat bran	50.0	33.0	[a]
Corn meal	20.0	—	[a]
Brewers' dried grain	—	40.0	—
Factors			
Protein	15.3	19.0	15.0
Fat	3.8	3.0	3.0
Fiber	12.6	20.0	5.0
Ash	6.3	8.0	13.7
Calcium	4.9	4.0	5.1

[a] Proprietary information, but comparable to that placed in other treatments.

Materials and Methods

Acquisition of Flies. At a 100 bird caged-layer poultry house at the Coastal Plain Experiment Station in Tifton, GA, we collected 10–20 female soldier flies probing the manure surface with their ovipositors and placed them in a 0.5-liter glass jar with a 2 by 3-cm roll of corrugated cardboard as an oviposition substrate (Booth and Sheppard 1984). After 24 h, the cardboard containing soldier fly eggs was placed in another 0.5-liter Sweetheart plastic cup (Sweetheart Cup Company, Chicago, IL) covered with a dry paper towel, and stored in a rearing room (27°C, 60–70% RH, and a photoperiod of 14:10 [L:D] h) until larvae emerged 4 d later. Once larvae were observed, 50 g of a 15% protein laying hen ration (Country Acres Feed, Brentwood, MO) mixed with 90 ml of water (70% moisture) was placed in the container. The larvae were allowed to feed on the medium for 4 d before being used in the experiment.

Wild Fly Population. Black soldier fly prepupae were collected from swine and poultry units located in Tifton, GA, and held in the above mentioned rearing room in six 1-liter clear Sweetheart plastic cups at a density of ≈500 per cup. Prepupal and adult characteristics compared across diet treatments were compared with data recorded for the wild population (see below).

Experimental Design. The following three diets were evaluated (Table 1): (1) Gainesville diet, which was developed for rearing house flies (Hogsette 1985) and the diet currently suggested for mass rearing the black soldier fly (Sheppard et al. 2002); (2) CSMA, an artificial rearing media for house fly larvae (Chemical Specialties Manufacturers' Association, Ralston Purina, St. Louis, MO); (3) the 15% protein layer hen ration, which had been used in preliminary trials for rearing *H. illucens.*

The experiment was replicated three times from April through October 1999. Preliminary studies using the layer hen ration rate of 10 g mixed with 17 ml water to 300 larvae daily resulted in the heaviest final larval weight. Therefore, this rate was selected as the feeding rate to be used for all three diets. The layer hen ration and Gainesville diet mixed with water had initial moisture levels of 70%, whereas the CSMA diet moisture was slightly lower at 64%. For each diet during an experiment, 300 4-d-old soldier fly larvae were placed in each of three 1-liter clear plastic cups. Cups were each covered with a paper towel and held in the rearing room. Feeding was terminated in a treatment when a cumulative 40% of the larvae in the three cups reached the prepupal stage. However, daily observations continued until all larvae had entered the prepupal stage or died. Prepupae were identified by a change in integument color from larval white to black (May 1961).

Immature Life-History Traits. Larval weight in each treatment was determined daily by selecting 10 larvae from each cup per treatment and weighing them individually on a Mettler AT261 DeltaRange balance (Mettler-Toledo, Hightstown, NJ). After weighing, larvae were returned to their respective cups. Final larval weight was defined as the average larval weight recorded on the day when 40% of all individuals in a treatment reached the prepupal stage.

Prepupae were removed daily and transferred to another 1-liter cup (containing 100 g white sand as a pupation medium) designated to hold prepupae from that particular replicate of a diet treatment. Additionally, each day, three of the prepupae collected from each replicate of each treatment were weighed and placed in petri plates and stored at −15°C for later determination of caloric content. Cups containing prepupae were covered with 50 by 50 cm of mosquito netting held in place with a rubber band, placed in the rearing chamber, and monitored daily for adult emergence. Percentage of larvae reaching the adult stage was recorded for each diet treatment. This could not be determined for the wild population, which was sampled when flies reached the prepupal stage. Days from egg collection to adult emergence were recorded for each fly reared on the diets.

Prepupal Calorie Content. Mean caloric content of prepupae per treatment was determined using bomb calorimetry (combustion) techniques (Dutcher 1983). Frozen prepupae were held from seven to 14 d in a convection oven set at 55°C. Individual dried prepupae were then weighed on a Mettler EA 100 electronic balance (Metler-Toledo), ground to ≈1-mm pieces, mixed with calorimeter grade benzoic acid (Sigma, St. Louis, MO) (1:10 specimen weight: benzoic acid weight) and compressed into a pellet. We were unable to make pellets with prepupae collected from the wild. These prepupae, unlike those reared on the diet treatments, appeared to contain greater amounts of fats and attempts to crush oven-dried specimens resulted in observable loss of materials. Therefore wild prepupae were analyzed without being mixed with benzoic acid. To ensure that this difference in techniques did not influence the results, caloric content was determined for prepupae from each diet treatment prepared with and without benzoic acid. A Parr oxygen bomb calorimeter (model No. 1341) (Parr Instrument, Moline, IL) was used to determine caloric content of pellets. Caloric content per mg ash-free dry weight per pre-

pupa was determined for each diet treatment and for the wild population.

Adult Life-History Traits. Weight, sex, and time from oviposition to adult emergence were recorded for each adult from the diet treatments. Individual adults were placed in 35-ml Solo cups (Solo, Urbana, IL) capped with a breathable lid. Half of the adult flies were provided 0.125 ml water daily via a 1.25-cm needle inserted through the lid. The remaining flies were held in similar conditions, but without water. Longevity was recorded for both groups.

Egg Development and Clutch Size. Initially, we hypothesized that larval media influences the number of eggs produced by black soldier flies and that mating was not required to produce eggs. Therefore, to test this hypothesis and determine the number of eggs per individual, a sample of nonmated females from each diet treatment and from the wild population was dissected in saline solution in a petri plate 1–4 d after emergence. Ovaries were removed and the number of developed eggs recorded. Specimens were dissected and examined under a Leica2000 Zoom dissecting microscope (Leica, Buffalo, NY). A fully developed egg was defined as elongate and creamy to white in color, while an oocyte was defined as spherical and transparent. Oviposition by females in 35-ml cups was also recorded to determine if the number of eggs in dissected specimens was similar to the number deposited by females reared on the same diet.

Dissected, unmated specimens did not contain developed eggs. Therefore, we suspected that mating was required for egg production. To test this hypothesis, ≈500 (<24 h postemergence) black soldier flies were collected from a colony (larvae fed Gainesville diet) and released at 1500 hours in a 2 by 2 by 3-m cage in a greenhouse maintained at ≈30°C. Observations and collection of mating pairs were made hourly beginning at 1600 hours on the day the adults were released and continued daily from 0800 to 1700 hours. Fifty-five mating pairs were collected by the conclusion of the second day. Mated females were weighed within 1 h of mating, placed in capped 35-ml cups, and held in the rearing room and provided water as previously described. We determined in a previous experiment that oviposition generally occurred 2 d after mating (Tomberlin 2001). Therefore, 2 d after mating, the ovaries of 45 mated females were dissected and percent with developed eggs determined. Number of developed eggs per individual was also recorded.

The remaining 10 females were allowed to oviposit in corrugated cardboard taped to the opening of the 35-ml cup. These eggs were removed and the number determined based on mass weight (Booth and Sheppard 1984). The estimated number of eggs deposited in the cardboard was compared with the number of eggs recorded for dissected mated females.

To determine the number of eggs oviposited by adults reared on each of the three diets and from the wild population, we released ≈500, <24 h old, adults from each treatment into 2 by 2 by 3-m cages placed in the greenhouse previously described. Each treatment had a separate cage. To collect egg masses, a 5-liter bucket (Plastic Packaging, West Springfield, MA) containing ≈1 kg Gainesville diet saturated with water was placed on a cinder block (40 cm high) in each cage to attract ovipositing individuals. Methods for collecting eggs were adapted from Booth and Sheppard (1984). Three layers of corrugated cardboard (each flute opening measured 1 by 4 mm) were glued together, cut into 5.0 by 2.5 by 1.0-cm blocks, and taped inside the 5-liter bucket ≈3 cm above the media. These cardboard blocks were replaced daily. An egg clutch was defined as a flute containing >100 eggs. Egg clutches collected each day from each treatment were weighed and stored in vials containing 80% ethanol until the eggs could be counted.

Egg Collection System. We suspected that eggs per flute did not accurately represent the number of eggs oviposited per individual. Therefore, we conducted an experiment to evaluate the relationship between flute dimensions and eggs deposited per flute by black soldier flies reared in our colony and held in a 2 by 2 by 3-m cage placed in the greenhouse. We examined three cardboard flute sizes; one with a smaller opening (1 by 3 mm); one with the same opening (1 by 4 mm); and the third with a larger opening (2 by 5 mm) than that used in the diet experiments. Cardboard blocks were collected and replaced daily. Eggs from each flute were stored in a vial containing 80% ethanol. Egg number per flute was determined as described above.

Statistical Analysis. Procedure GLM (SAS Institute 1992) was used to analyze the recorded data. Least significant difference (LSD) test (SAS Institute 1992) was used following a significant F test ($P \leq 0.05$) to separate mean differences between diet treatments, and the wild population for: percent survival to adult stage, percent females and males to emerge, pupal skin weights, adult male and female weights, and male and female longevity with and without water. Additionally for the diet treatments only, the previously described procedure was used to separate mean larval and pupal development periods and final larval weight. Percentage values were normalized by arcsine transformation.

Mean egg number and total weight of eggs per flute were analyzed using the procedures previously described. Regression and Pearson's correlation analysis (SAS Institute 1992) were used to determine the relationship between egg number and mass weight per flute for each treatment, and adult weight and longevity.

Results

Immature Life-History Traits. Final larval weight across treatments ranged from 0.153 to 0.171 g (Table 2) and did not differ significantly ($F = 2.35$; df = 2, 2; $P > 0.2118$). Survivorship of larvae to the prepupal stage was not significantly different across diet treatments ($F = 1.07$; df = 2, 23; $P > 0.3592$) and ranged from 96.0 to 97.8% (Table 3). Time from egg to prepupal stage per treatment ranged from 22.5 to 24.1 d (Table 4) and did not differ significantly ($F = 0.74$; df = 4, 4; $P > 0.6121$). Mean prepupal weights differed significantly among diet treatments including the wild

Table 2. Comparison of larval, prepupal, pupal skin, and adult weights (grams), and prepupal caloric content per milligram of ash-free dry weight for *H. illucens* reared on three diets and from field-collected prepupae

Diet	Final larval weight	Prepupal weight	Caloric content/mg	Pupal skin weight	Adult weight	
					Male	Female
Gainesville diet	0.157 ± 0.077A *n* = 3	0.104 ± 0.027A *n* = 30	3.51 ± 0.28A *n* = 23	0.011 ± 0.003A *n* = 40	0.046 ± 0.005A,a *n* = 272	0.056 ± 0.005A,b *n* = 339
CSMA	0.153 ± 0.063A *n* = 3	0.107 ± 0.041A *n* = 30	4.21 ± 0.39AB *n* = 22	0.011 ± 0.002A *n* = 45	0.044 ± 0.005A,a *n* = 254	0.054 ± 0.005A,b *n* = 320
Layer hen ration	0.171 ± 0.043A *n* = 3	0.111 ± 0.034A *n* = 30	4.48 ± 0.27B *n* = 20	0.016 ± 0.006B *n* = 45	0.053 ± 0.007B,a *n* = 234	0.064 ± 0.006B,b *n* = 316
Wild population	NA	0.220 ± 0.040B *n* = 30	5.95 ± 0.32C *n* = 15	0.025 ± 0.008C *n* = 30	0.085 ± 0.016C,a *n* = 57	0.111 ± 0.022C,b *n* = 70

Means within a column followed by different capital letters are significantly different. Means for both sexes with different lowercase letters within a treatment differ significantly ($P \leq 0.05$; LSD, SAS Institute 1992). NA, Not applicable.

population ($F = 146.79$; df = 3, 116; $P < 0.0001$) and ranged from 0.104 to 0.220 g (Table 2). Pupal skins accounted for ≈10% of their weight (Table 2). Prepupae reared on layer hen ration had the greatest numerical weight among diet treatments, but still weighed significantly less than prepupae from the wild populations. Prepupal skin weight differed significantly between diet treatments ($F = 75.47$; df = 3, 156; $P \leq 0.0001$) with skins from specimens reared on layer hen ration and from the wild population weighing the most.

Prepupal Calorie Content. Mean calorie content per mg ash-free dry weight per prepupa was significantly different across treatments ($F = 8.70$; df = 3, 76; $P \leq 0.0001$) and ranged from 3.51 to 5.95 cal per mg ash-free dry weight, with those specimens collected from the wild having the greatest calorie content (Table 2). Wild prepupae weighed more and had a higher concentration of fat, yielding ≈3.5 times more calories, than prepupae reared on the diet treatments. Prepupae reared on the diets contained ≈365 calories, whereas the wild prepupae contained an average of 1,309 calories. No significant differences were determined for the caloric content of prepupae prepared with or without benzoic acid.

Adult Life-History Traits. Mean adult emergence rate (Table 3) differed significantly ($F = 26.84$; df = 3, 27; $P \geq 0.0001$) and ranged from 21.7 to 27.2% for the diet treatments, whereas 91.3% of the prepupae sampled from the wild yielded adults. Of those to emerge, 55.2–60.5% were female (Table 3) with no significant difference across diet treatments or the wild population ($F = 1.05$; df = 2, 22; $P > 0.3660$). Male black soldier flies reared on diets were significantly smaller than females ($F = 493.59$; df = 7, 1854; $P \leq 0.0001$) reared on the same diet. This size differential also occurred in the wild population (Table 2). However, when comparing the same sex across treatments, wild males and females were significantly larger than their diet-reared counterparts. Although not significantly different ($F = 9.92$; df = 7, 10; $P > 0.2875$), adult males generally emerged earlier than females (Table 4).

Table 3. Percent survival of *H. illucens* larvae to the prepupal and adult stages and sex ratio for larvae reared on three diets and for prepupae from a wild population

Diet	*n*	Larval survivorship to prepupae	Adult emergence from prepupae	Sex ratio (% female)
Gainesville diet	8	97.8 ± 0.6A	27.2 ± 6.7A	60.5 ± 1.2A
CSMA	9	96.0 ± 1.4A	23.9 ± 4.0A	55.2 ± 2.0A
Layer hen ration	9	96.1 ± 0.4A	21.7 ± 1.8A	58.0 ± 3.4A
Wild population	6	NA	91.3 ± 4.8B	56.0 ± 0.0A

Means within a column followed by different letters differ significantly ($P \leq 0.05$; LSD, SAS Institute 1992). NA, not available.

An interaction effect was determined for larval diet and the provision of water on adult longevity ($F = 48.22$; df = 15, 1,764; $P \leq 0.0001$) of black soldier flies (Table 4). Adult males reared on a diet and provided water as adults lived 9.3–9.7 d, whereas those not provided water lived 6.0–7.1 d. Females reared on the treatments and provided water as adults lived 7.9–8.5 d, whereas those not provided water lived 6.1–6.4 d. Males and females that emerged from wild-collected prepupae lived significantly longer than those reared on the artificial diets. Wild males and females lived ≈14 d when provided water as adults and 7.8 and 8.2 d, respectively, when not provided water. Male and female longevity within a treatment when not provided water did not differ. Longevity of adults provided water was significantly correlated with individual weight ($r^2 = 0.40$; $P \leq 0.0001$).

Egg Development and Clutch Size. Twenty virgin females per treatment, and four from the wild population, from 1 to 4 d postemergence were dissected and examined for mature eggs, but none were found (Fig. 1 a and b). For each treatment, including the wild population, <1% of the virgin females placed in plastic medicine cups laid eggs. None of these eggs hatched. Thirty-two (72%) of the 45 mated-colony females that were dissected 2 d after mating (Fig. 1c) had completely formed eggs. Number of eggs per individual ranged from 323–621, which accounted for ≈13–26% of their body weight. Six of the 10 mated females from the colony that were held individually in 35-ml cups deposited eggs. The number of eggs laid per individual ranged from 206 to 639, which accounted for 7.9–23.4% of their body weight. Individuals dissected 3 d after laying eggs (Fig. 1d) had no additional ovarian development and little fat body present.

Egg Collection System. Mean eggs per flute ($F = 0.72$; df = 3, 71; $P > 0.5456$) and weight of eggs per flute

Table 4. Selected life-history traits of *H. illucens* reared on three diets and for adults reared from field-collected prepupae

Diet treatment	Longevity, d adults provided water		Longevity, d adults not provided water		Development, d from egg to prepupa	Development from egg to adult, d	
	Male	Female	Male	Female		Male	Female
Gainesville diet	A9.3 ± 0.4A,a *n* = 106	A7.9 ± 0.2A,a *n* = 161	B6.0 ± 0.2A,a *n* = 159	B6.1 ± 0.1A,a *n* = 160	22.5 ± 0.7A *n* = 3	43.0 ± 2.9A,a *n* = 3	43.4 ± 2.1A,a *n* = 3
CSMA	A9.7 ± 0.4A,a *n* = 103	A8.5 ± 0.2A,a *n* = 163	B5.9 ± 0.2A,a *n* = 145	B6.2 ± 0.2A,a *n* = 138	23.4 ± 0.3A *n* = 3	43.0 ± 2.5A,a *n* = 3	43.0 ± 1.3A,a *n* = 3
Layer hen ration	A9.3 ± 0.4A,a *n* = 96	A8.5 ± 0.3A,a *n* = 151	B7.1 ± 0.2B,a *n* = 140	B6.4 ± 0.2A,a *n* = 138	24.1 ± 0.9A *n* = 3	40.4 ± 2.4A,a *n* = 3	41.7 ± 2.1A,a *n* = 3
Wild population	A14.3 ± 1.2B,a *n* = 25	A14.2 ± 0.9B,a *n* = 42	B7.8 ± 0.4B,a *n* = 31	B8.2 ± 0.4B,a *n* = 22	NA	NA	NA

Means within a column followed by different capital letters differ significantly. Means for both sexes within a treatment with different lower case letters differ significantly. Longevity means for a sex provided water and not provided water preceded by different capital letters differ significantly ($P \leq 0.05$; LSD, SAS Institute 1992). NA, Not available.

($F = 0.83$; df = 19, 20; $P > 0.4798$) were not significantly different among diet treatments, including the wild population (Table 5). Individual eggs ranged in weight from 0.23 to 0.25 mg and mean number of eggs per flute ranged from 603 for adults reared on Gainesville diet and the wild population to 689 for adults reared on layer hen ration. Mean weight of eggs per flute (clutch weight) ranged from 0.0145 g from adults reared on the Gainesville diet to 0.0159 g for adults reared on the CSMA larval fly diet. Correlations between mean egg weight and number of eggs per flute for adults reared on each diet and the wild population were significant ($P < 0.05$) (Table 5). The regression analysis for mean egg number versus egg clutch weight per flute size was also significant for all treatments including the wild population (Table 5).

The inability to determine a difference in the size of egg clutches per diet treatment and the wild population was due to the early misconception that one flute held the eggs of one female (Booth and Sheppard 1984). The number of eggs deposited per flute was limited by flute size. The number of eggs deposited in the smaller flute (1 by 3 mm) averaged 431 eggs per flute, whereas those in the larger flute (2 by 5 mm) averaged 1,157 eggs per flute. Based on measurements of the depths that eggs were deposited in the different sized flutes, individuals were able to insert their abdomen and ovipositor ≈1 cm into the larger flute and ≈0.7 cm in the smallest flute. Egg size was not significantly different across diet or flute treatments ($F = 0.83$; df = 3, 71; $P > 0.4798$).

Discussion

All three diets are suitable for rearing the black soldier fly. They are nutritionally similar, which probably explains why final larval weight and caloric content of diet-reared prepupae were comparable. However, lab-reared prepupal weight differed from the wild prepupae sampled, which might be due to wild larvae having access to additional nutrients (Slansky and Scriber 1985, Dicke et al. 1989), such as the continuous stream of fresh manure in poultry facilities, not mixed with old resources as in our tests. Recent laboratory studies determined that black soldier fly larvae fed 5-d-old hen manure grew at half the rate of larvae fed 18 h old manure (D.C.S., unpublished data). Weight differences recorded for prepupae reared on laying hen ration and those reared on the other diets might be attributable to differences in calcium content (Table 1). Soldier fly larvae sequester ingested calcium and convert it to calcium carbonate, which is secreted through the hypodermis and covers the larval integument (Johannsen 1922).

Development time from egg to prepupae for the black soldier fly in our study was six to eight days shorter than that recorded by May (1961) who reported a mean development of 31 d under similar temperature and humidity conditions. Differences between the two studies might be due to various factors, such as different larval densities (Morrison and King 1977) or food quality (Slansky and Scriber 1985, Dicke et al. 1989). Furman et al. (1959) suggested these factors could delay black soldier fly larval development up to four months. However, May (1961) did not provide detail sufficient for comparison.

Differences in percent emergence per diet treatment and those collected from the wild might also be due to larval diet and being held in a sub-optimal habitat. Larvae in our experiment were held and fed in containers that resulted in continuous contact with their excreta. Sheppard (1983) determined that wild soldier fly larvae remain on the surface of the wastes accumulating below layer facilities and feed on fresh manure as it is produced. Manure digested by the larvae then accumulates below the larvae. Because the soldier fly larvae in our experiment were held in closed containers, they fed on media that was mixed with diet residue and their own waste. Therefore, the soldier fly larvae might have been forced to feed to a degree on their own wastes, which we suspect they normally avoid. Larvae of other dipteran species, such as the house fly, need fresh manure daily for optimal growth (Morgan and Eby 1975). This need for fresh manure is because anaerobic organisms digest manure as it ages, resulting in fewer nutrients for the larvae and thereby suppressing larval growth (Beard and Sand 1973). Developmental time from egg to the adult did not differ between sexes for wild black soldier flies, as well as those reared on diet in the laboratory.

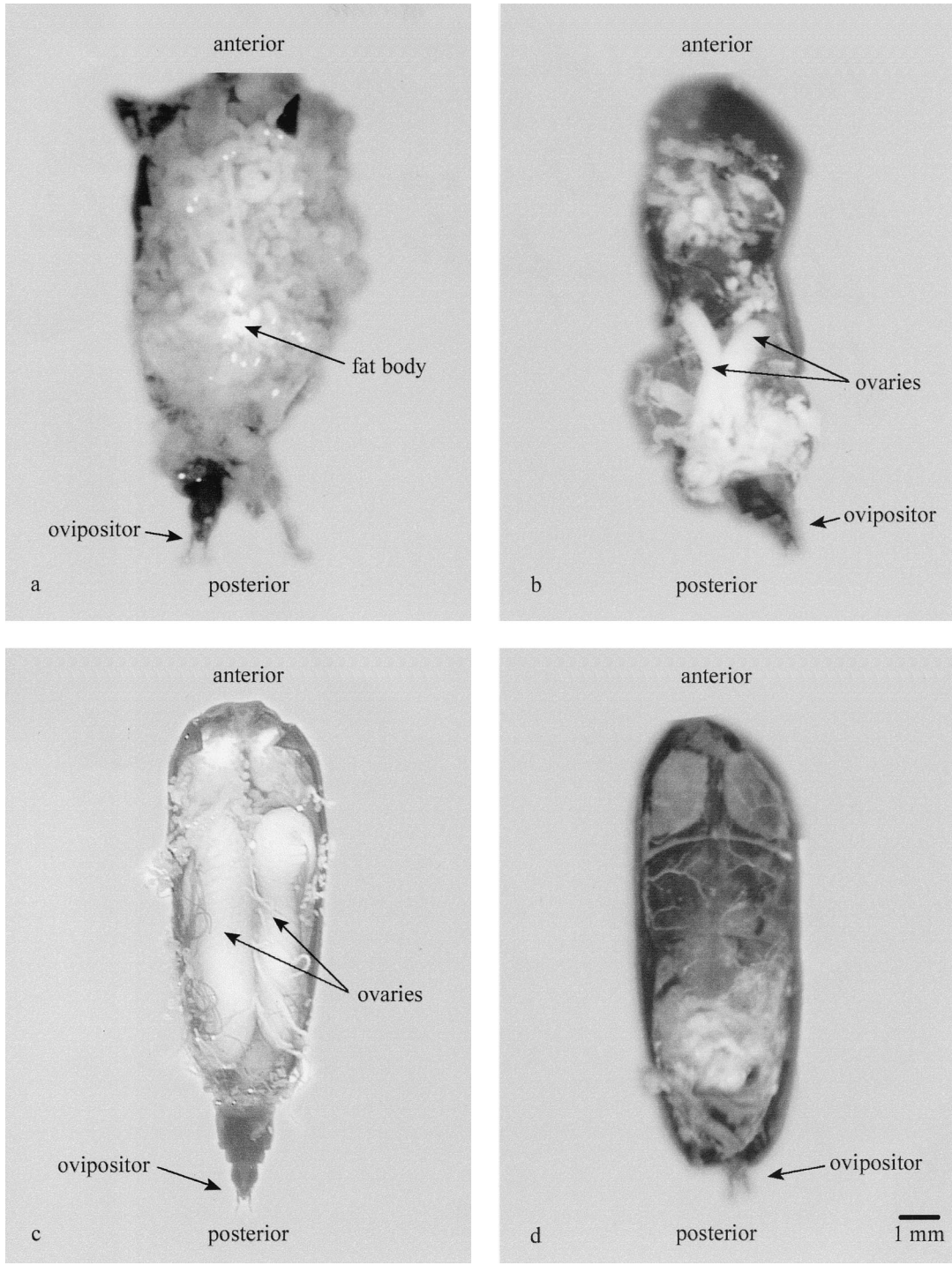

Fig. 1. Ventral view of the dissected abdomen of a female black soldier fly. (a) Freshly emerged (<24 h) with fat body present; (b) freshly emerged (<24 h) with fat body removed; (c) 2 d after mating remaining fat body intact; (d) 3 d after laying eggs with remaining fat body intact.

Water, unlike food, is essential for adult black soldier flies to reproduce (Sheppard et al. 2002), which might be due to the less vigorous and dehydrated adults being unable to mate effectively and therefore not laying viable eggs. We determined that individuals reared on the diets and provided water lived 1–2 d

Table 5. Comparison of clutch weight (grams), and egg weight (milligrams) for *H. illucens* reared on three diets and for field-collected prepupae and the correlation and regression analyses for clutch weight (milligrams) and eggs per clutch per treatment

Treatment	Correlation[a]	Regression models for eggs per clutch	Clutch weight	Egg weight
Gainesville diet $n = 20$	$r^2 = 0.88$, df = 20	= 173.87 + 29,372 (clutch weight) $F = 62.8$; df = 1, 18; $P < 0.0001$	0.0145 ± 0.00012A	0.24 ± 0.012A
CSMA $n = 15$	$r^2 = 0.90$, df = 15	= 143.15 + 31935 (clutch weight) $F = 55.5$; df = 1, 13; $P < 0.0001$	0.0159 ± 0.00018A	0.25 ± 0.011A
Layer ration feed $n = 20$	$r^2 = 0.93$, df = 20	= 124.64 + 35346 (clutch weight) $F = 122.3$; df = 1, 18; $P < 0.0001$	0.0158 ± 0.00012A	0.23 ± 0.008A
Wild population $n = 20$	$r^2 = 0.98$, df = 20	= 25.12 + 38887 (clutch weight) $F = 686.8$; df = 1, 18; $P < 0.0001$	0.0153 ± 0.00012A	0.25 ± 0.004A

[a] Pearson's correlation, significance set at $P \leq 0.05$ (SAS Institute 1992).
Means within a column followed by different letters differ significantly.

longer than those not provided water. In contrast, wild adult soldier flies provided water lived 4 d longer than adults reared on the diets. This significant difference in longevity might be explained by caloric content of the prepupae. Prepupae reared on the diet treatments contained ≈365 cal, whereas the wild prepupae contained 1,309 cal per prepupa. The additional calories provided energy that might have resulted in increased longevity of the wild adults.

Egg development studies were problematic because of misconceptions concerning the definition of a black soldier fly egg clutch, or eggs oviposited by one individual. Booth and Sheppard (1984) stated that the average number of black soldier fly eggs per clutch was 998 ± 78 (mean ± SE). They collected eggs using the openings in corrugated cardboard (flutes) as the oviposition site. Before Booth and Sheppard (1984), researchers reported black soldier fly egg clutches with 119–502 eggs (Gonzalez et al. 1963) and 205–802 (Stephens 1975) in dried hen manure and on bananas, respectively, which are similar to our eggs per clutch data determined for individuals dissected 2 d after mating.

Methods described by Booth and Sheppard (1984) for collecting black soldier fly eggs are suitable. However, these methods are not recommended for estimating clutch size for individual soldier flies. Egg clutches from diet-reared and wild adults were smaller than those recorded by Booth and Sheppard (1984), but individual egg size was similar. The reduction in egg number per clutch for our experiment and that recorded by Booth and Sheppard (1984) is most likely due to flute size, which we determined can limit the number of eggs deposited per flute. Therefore, our results really estimate number of eggs per flute, which also might have been the case for Booth and Sheppard (1984). However, the flute size they used is unknown. We suspect that multiple individuals could deposit eggs in a single flute, which would skew clutch size estimates. Egg clutch weight varied <1% when allowing individuals to oviposit in cardboard flutes of equal size. However, egg clutches oviposited by mated individuals collected from the black soldier fly colony and placed in 35-ml cups and those dissected 2 d after mating varied as much as 75%. We hypothesize dissecting females 2 d after mating provides an accurate estimate of the total number of eggs produced by a female. Additionally, oviposited eggs might not be as accurate due to variables influencing number of eggs produced, such as time from emergence to mating. Rogers and Marti (1994) determined that the age of female fall armyworms, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), at first mating significantly influences reproductive potential and that extended female virginity resulted in reduced fecundity and fertility.

The black soldier flies in our studies reproduced without feeding and apparently relied on fat reserves acquired during larval development for adult survival and egg production (D.C.S., unpublished data). Therefore, any delay in mating could result in resources being reallocated from producing eggs to prolonging the adult stage. Similar to our hypothesis for the black soldier fly, Chippindale et al. (1993) determined that food quality was directly related with egg production and inversely related to adult longevity for *Drosophila melanogaster* Meigen (Diptera: Drosophilidae). Higher quality food resulted in greater egg production, but reduced longevity in fruit flies. Additionally, the number of times a female arthropod mates can influence the number of eggs deposited. As suggested by Foster and Ayers (1995) for female *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), mating more than once might be attributed to male deficiencies, but might result in greater numbers of eggs being fertilized and deposited.

Most of the literature on the black soldier fly is restricted to its use as a biological control agent of house flies and as a manure management agent in poultry facilities. Our study provides additional information on the life history of this species reared on three diets, as well as for those collected from the wild. Such information is necessary for developing its potential as a biological control and waste management agent in livestock and poultry production. The three diets examined in this study are suitable for rearing black soldier flies. However, because of the large differences between wild and laboratory-reared specimens, further research is needed to refine and improve larval rearing for mass production of this species.

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