Development of the Black Soldier Fly (Diptera: Stratiomyidae) in Relation to Temperature

JEFFERY K. TOMBERLIN,[1] PETER H. ADLER,[2] AND HEIDI M. MYERS[3]

Environ. Entomol. 38(3): 930–934 (2009)

ABSTRACT The black soldier fly, *Hermetia illucens* L., was reared on a grain-based diet at 27, 30, and 36°C. Survival of 4- to 6-d-old larvae to adults averaged 74–97% at 27 and 30°C but was only 0.1% at 36°C. Flies required a mean of ≈4 d (11%) longer to complete larval and pupal development at 27°C than at 30°C. At 27 and 30°C, females weighed an average of 17–19% more than males but required an average of 0.6–0.8 d (3.0–4.3%) longer to complete larval development. At both temperatures, adult females lived an average of ≈3.5 d less than adult males. The duration of larval development was a significant predictor of adult longevity. Temperature differences of even 3°C produce significant fitness tradeoffs for males and females, influencing life history attributes and having practical applications for forensic entomology.

KEY WORDS black soldier fly, *Hermetia illucens*, development, temperature

The black soldier fly, *Hermetia illucens* L. (Diptera: Stratiomyidae), develops in decomposing organic matter in temperate and tropical areas of the world. Adults do not feed, except to take water, acquiring the nutrition necessary for reproduction during larval development (Tomberlin et al. 2002). Males aggregate at lekking sites, where they encounter flying females (Tomberlin and Sheppard 2001). Within 2 d of mating, females produce 320–620 eggs, oviposit in decomposing organic matter, and die within hours (Tomberlin et al. 2002). Three generations are produced annually in the southeastern United States (Sheppard et al. 1994).

The black soldier fly is economically important in confined animal facilities, and prepupae can be used as animal feed. House flies, *Musca domestica* L. (Diptera: Muscidae), are suppressed when manure is colonized by black soldier flies, and poultry wastes are reduced 42–56% by larval feeding (Furman et al. 1959, Axtell and Arends 1990, Sheppard et al. 1994). Prepupae of black soldier flies are high in protein and fat and can be self-harvested and used as food for fish (Bondari and Sheppard 1981) and swine (Newton et al. 1977).

Because the black soldier fly will colonize human remains, development data can be used in forensic studies to estimate the period of insect activity (PIA) (Lord et al. 1994, Tomberlin et al. 2005, Pujol-Luz et al. 2008). More information, however, is needed on life history characteristics under varying environmental conditions before the PIA can be used routinely in forensic cases.

Although life history traits have been examined for black soldier flies reared on different diets (Tomberlin et al. 2002), no data are available on the effects of temperature on development. The objective of our study was to examine the life history traits of black soldier flies reared at three different temperatures. To examine the relation of immature development features (e.g., duration) to adult fitness characters, we tracked individual development from larva to adult.

Materials and Methods

Source of Flies. Black soldier flies were obtained from a colony maintained year-round in an outdoor greenhouse at the Texas Agricultural Experiment Station (TAES), Stephenville, TX. The TAES colony was established in fall 2003 from the eggs of a laboratory colony at the Coastal Plain Experiment Station, University of Georgia, Tifton, GA, which originated from material collected at a poultry facility in Bacon Co., GA, in 1998. The TAES colony was supplemented with wild females taken from a swine facility in Erath Co., TX, in spring 2004.

Experiment Design. Eggs for each replicate were collected on the day of oviposition from blocks of dry, corrugated cardboard held in an outdoor greenhouse (Sheppard et al. 2002). These eggs, recovered from a minimum of six females per replicate, were placed on 100 g of a grain-based diet (dry matter: 20% corn meal, 30% alfalfa meal, 50% wheat bran) (Hogsette 1992) with 70% moisture and maintained at 27°C and 60% RH in an E-30B Percival Growth Chamber (Percival, Boone, IA). The grain-based diet was selected as the

---

[1] Corresponding author: Department of Entomology, Texas A&M University, College Station, TX 77843 (e-mail: jktomberlin@ag.tamu.edu).

[2] Department of Entomology, Soils and Plant Sciences, Clemson University, Clemson, SC 29634.

[3] Department of Animal Science, Tarleton State University, Stephenville, TX 76401.

0046-225X/09/0930–0934$04.00/0

Table 1. Life history data for laboratory-reared black soldier flies at three temperatures, based on material from a colony maintained at the Texas Agricultural Experiment Station, Stephenville, TX

Temperature (°C)	Sex	Larval development[a] (d)	Prepupal weight (g)	Pupal development (d)	Adult weight (g)	Adult longevity (d)
27	Female	20.1 ± 0.32	0.160 ± 0.0131	17.8 ± 0.74	0.081 ± 0.0073	14.0 ± 0.69
27	Male	19.5 ± 0.30	0.139 ± 0.0119	17.9 ± 0.79	0.066 ± 0.0057	17.4 ± 0.94
30	Female	18.5 ± 0.50	0.148 ± 0.0038	15.5 ± 0.58	0.076 ± 0.0029	12.4 ± 0.70
30	Male	17.7 ± 0.52	0.128 ± 0.0029	15.4 ± 0.63	0.063 ± 0.0021	15.9 ± 1.03
36	Combined[b]	25.9 ± 0.23	0.085 ± 0.0029	—	—	—

Values are means ± SE representing three replicates, 2003–2004.

[a] Larval development times were measured from the day of hatching; sex was determined at adult emergence. Experiments began with 300 larvae (4–6 d old) in each of two containers within each of three replicates per temperature, for a grand total of 1,800 larvae initially at each temperature.

[b] Although 73.4% of larvae reared at 36°C survived to the prepupal stage, only 0.1% of the original 1,800 became adults; separate male and female values, therefore, could not be reported and are combined.

larval medium because of its use in standard colony maintenance (Sheppard et al. 2002). Neonate larvae were held at 27°C for 4–6 d to reduce mortality from handling and then distributed to three different temperature treatments.

Larvae were reared at 27, 30, and 36°C in the Percival growth chambers. Temperatures selected for study encompassed those from the higher range experienced by black soldier flies in temperate areas and used in colony maintenance (Sheppard et al. 1994, 2002). The experiment was replicated three times (October–November 2003, April–June 2004, October–November 2004), with two containers per replicate within each temperature (27, 30, and 36°C). In each temperature treatment, 300 4- to 6-d-old larvae were placed in a 1-liter clear plastic container covered with a paper towel. Each temperature treatment, therefore, began with 300 larvae in each of two containers per each of three replicates. Containers were randomized as to shelf within rearing chambers, and temperature treatments were randomized among chambers across replicates. Ten grams of diet mixed with 17 ml of water were added daily to each 1-liter container. The addition of new food was terminated for each container when 40% of the larvae in that container had reached the prepupal stage, as indicated by a darkening of the integument. Daily observations continued until all larvae entered the prepupal stage or died. Continued addition of food beyond this point can cause high mortality (J.K.T., unpublished data).

Life History. Larval development time was recorded from the day of hatching until the day that each larva became a prepupa. New prepupae were removed daily from each replicate, individually weighed, transferred to individual 35-ml cups with a breathable lid and identifying information, and returned to their respective growth chamber. The percentage of 4- to 6-d-old larvae reaching the adult stage was recorded for each container within a replicate and temperature.

The sex and live weight of each adult were recorded on the day of emergence. Adult flies were provided 0.125 ml of water daily on the bottom of their containers using a 1.25-cm needle inserted through the lid. Longevity, from the day of emergence to the day of death, was recorded individually for males and females. Voucher specimens (larvae and adults) from each replicate were deposited in the Texas A&M University Insect Collection, College Station, TX.

Statistical Analysis. Development times of larvae and pupae, prepupal and adult weights, and adult longevity were subjected to analysis of variance (ANOVA), with sex and temperature as main effects, replication as a random factor, and container nested within temperature. Because only 0.1% of the entire lot of 1,800 larvae produced adults at 36°C, this temperature treatment was not included in statistical analyses. To determine whether adult weight and longevity were related and whether adult weight and longevity could be predicted from larval development time, we used stepwise regression ($\alpha = 0.05$, forward and backward selection), with temperature and sex (0 = female, 1 = male) as dummy variables. Sex ratios for each container within a replicate and temperature were evaluated with a χ^2 test. All statistical analyses were performed using Minitab (2007).

Results

Life History Traits of Immatures. The main effects of temperature ($F = 66.39$; df = 1,16; $P < 0.001$) and sex ($F = 11.95$; df = 1,16; $P = 0.003$) significantly influenced larval development. The interaction of temperature and sex was not significant ($F = 0.07$; df = 1,16; $P = 0.790$). Male and female larvae reared at 27°C required an average of ≈1.7 d (8.6%) longer to reach the prepupal stage than did those reared at 30°C, and females required about half a day to a day (3–4%) longer overall than did males (Table 1). Development to the prepupal stage for larvae reared at 36°C required an average of 26 d, roughly 24 and 30% longer than at 27 and 30°C, respectively.

Prepupal weight differed significantly across sex ($F = 5.54$; df = 1,16; $P = 0.032$) but not across temperature ($F = 1.74$; df = 1,16; $P = 0.206$) or in the interaction of sex and temperature ($F = 0.00$; df = 1,16; $P = 0.951$). Female prepupae weighed an average of ≈13% more than males at both temperatures (Table 1). The average prepupal weight of all individuals reared at 36°C was roughly 43 and 38% less than prepupae reared at 27 and 30°C, respectively.

Pupal development time differed significantly across temperature ($F = 11.18$; df = 1,16; $P = 0.004$) but not across sex ($F = 0.00$; df = 1,16; $P = 0.982$) or in the interaction of sex and temperature ($F = 0.03$; df = 1,16; $P = 0.861$). Males and females required an average of ≈2.5 d more to complete the pupal stage at 27°C than at 30°C (Table 1). At 36°C, only three larvae from the initial 1,800 entered the pupal stage.

Life History Traits of Adults. At 27 and 30°C, 83.2–91.8 and 74.2–96.7%, respectively, of the individuals per replicate survived to adults, whereas at 36°C, only 0.1% (two males) in the entire treatment survived. The male to female sex ratios at emergence did not differ from unity ($\chi^2 = 0.310$–3.642, df = 1, $P > 0.05$) and were independent of temperature for all replicates ($\chi^2 = 0.130$–1.843, df = 1, $P > 0.05$), ranging from 0.86 to 1.25 at 27°C and from 0.90 to 1.17 at 30°C. Mean weight loss from the prepupal to adult stage was greater for males than for females at both 27 (male weight loss: 52.5%, female: 49.4%) and 30°C (male weight loss: 50.8%, female: 48.6%).

Reflecting prepupal weight, adult weight also differed significantly across sex ($F = 8.44$; df = 1,16; $P = 0.010$) but not across temperature ($F = 12.08$; df = 1,16; $P = 0.013$) or in the interaction of sex and temperature ($F = 3.08$; df = 1,16; $P = 0.866$). At 27 and 30°C, females weighed 18.5 and 17.1%, respectively, more than did males (Table 1). The only two males that emerged at 36°C weighed 0.038 ± 0.0103 g or >40% less than males reared at 27 or 30°C. Larval development time was not a significant ($P > 0.05$) predictor of adult weight.

Sex significantly influenced adult longevity ($F = 14.85$; df = 1,16; $P < 0.001$), but neither temperature ($F = 0.20$; df = 1,16; $P = 0.088$) nor the interaction of temperature and sex was significant ($F = 0.01$; df = 1,16; $P = 0.936$). When reared at 27 and 30°C, males lived an average of ≈3.4 (19.5%) and 3.5 d (22.0%) longer, respectively, than did females (Table 1). The oldest males and females reared at 27°C lived 37 and 33 d, respectively, and at 30°C, 26 and 23 d, respectively. The two males that emerged from the 36°C treatment lived only 2 d. Larval development time was a significant predictor of adult longevity, with longevity increasing by about a day for each day of larval development (adult longevity = −6.88 + 1.04 larval development time + 4.16 sex; $F = 19.17$; df = 2,21; R^2[adj.] = 61.2%; $P < 0.0001$). Adult longevity increased with adult weight (adult longevity = 5.75 + 4.73 sex + 95.1 adult weight; $F = 13.70$; df = 2,21; R^2[adj.] = 52.5%; $P < 0.0001$).

Discussion

The black soldier fly is a tropical and warm-season temperate species (Sheppard et al. 1994), in accordance with its high survivorship to the adult at 27 and 30°C. Smaller adults and a shorter adult lifespan are associated with increasing temperature. Larvae of other flies, such as the blow fly *Chrysomya rufifacies* (Macquart), (Diptera: Calliphoridae) also produce smaller pupae and adults as temperature increases, possibly a result of starvation (Byrd and Butler 1997) associated with increased metabolism and growth rate.

The upper limit for development of the black soldier fly lies between 30 and 36°C; sustained temperatures of 36°C are beyond the optimal range of development. We recognize, however, that our colony material might be adapted to rearing temperatures of 27–30°C, the range used for routine colony maintenance of soldier flies (Sheppard et al. 2002). If so, selection for development at colony temperatures would have occurred within <6 yr of establishment of the original colony and within less than half a year of infusion with wild material. Although larvae reared at 36°C had a high probability (73.4%) of becoming prepupae, only 0.1% of the larvae pupated. Reduced survival at this life stage could be caused by failure of prepupae to attain the necessary critical weight. For example, larvae of the beetle *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae) that fail to reach a critical larval weight do not pupate (Keena 2005); the critical larval weight of *A. chinensis* (Forster) varies between and within populations (Adachi 1994).

The number of degree-days necessary to complete development can vary with available resources (Trudgill et al. 2005). Insects developing on high-quality resources require fewer degree-days to develop than those on lower quality resources (Amalraj et al. 2005, De Haas et al. 2006). Larval blow flies [*Calliphora vicina* Robineau-Desvoidy and *Lucilia sericata* (Meigen)] grow significantly faster on lung or heart tissue than on liver and on pig organs than on those of cow (Kaneshrajah and Turner 2004, Clark et al. 2006). Grain diets differ in composition and quality from animal tissue and manure, necessitating caution when using development data outside the context (e.g., diet) of the specific study.

Within an acceptable developmental temperature range, different temperature regimens produce fitness tradeoffs. For the black soldier fly, adults reared at 27°C weigh ≈5% more and live roughly 10% longer than those reared at 30°C. However, an average of 4 more d are required to complete larval development at 27°C than at 30°C. Because adults do not feed, other than to take water (Tomberlin et al. 2002), larval feeding is crucial to fitness. Females spend more time than males as larvae and weigh more as adults. The tradeoff is that, although longer larval development might allow more energy reserves to accumulate, resulting in greater fecundity (Tomberlin et al. 2002) and chances of securing a mate (Alcock 1990), the risk of larval disease, parasitism (Bradley et al. 1984), predation, resource degradation, and subsequent loss of mating opportunities could increase. Because females lay a single egg batch and die shortly thereafter (Tomberlin et al. 2002), size is potentially more important for fitness of the black soldier fly than is longevity. However, greater longevity could translate into an increased likelihood of locating a lek and securing a mate. This benefit might be especially important because mating depends on sunlight

(Tomberlin and Sheppard 2002) and typically would not occur during overcast periods.

Development data at 27°C for the black soldier flies in our study can be compared with data from the study of Tomberlin et al. (2002), who used the same diet and, with few modifications, the same rearing methods. Tomberlin et al. (2002) reported ≈43 d from egg to adult, which, assuming a 4-d egg stage (Booth and Sheppard 1984), would be similar to the 41.6-d overall mean for development from neonate larvae to adults in our study. Both males and females in our study had a higher rate of emergence from prepupae, weighed more, and lived longer than flies in the study of Tomberlin et al. (2002). The greater emergence rates might be attributable to isolation of prepupae from the feeding group in our study, rather than allowing them to develop and emerge communally. The greater adult weights in our study would have contributed to greater longevity, although the reasons for heavier adults are not evident. The introduction of Texas flies, presumably adapted to a different set of environmental conditions, into the original Georgia-derived colony might have contributed to differences in development. Parental flies were not held outdoors in the study of Tomberlin et al. (2002) but were in our study, although the effect, if any, of this difference is not clear. Environmental differences experienced by the parental generation, however, can affect life history traits such as development times and survival of the subsequent generation in a variety of insects (Hunter and McNeil 2000, Liu et al. 2004).

Developmental variation among studies of flies is common and can be attributed to factors such as experiment design (e.g., different diets and rearing densities) or adaptations of the source populations to local environmental conditions. The blow fly *Phormia regina* (Meigen), for example, is commonly used to estimate a minimum postmortem interval for human remains based on its PIA (Anderson 2000). However, development times for *P. regina* vary geographically (Kamal 1958, Greenberg 1991, Anderson 2000, Byrd and Allen 2001).

Differences among populations of the black soldier fly have practical implications in forensic cases. These differences could be particularly important for this species, which colonizes human remains over a broad geographic range in warm and cool months with intermittent warm periods (J.K.T., unpublished data), especially because both the parents and offspring will experience markedly different geographical and seasonal temperature regimens. Our study suggests that available life history data for the black soldier fly do not represent the full developmental range and, therefore, could introduce error in estimating the PIA on human remains.

Our results not only suggest caveats regarding the use of development data in forensic entomology but also can be used to refine colony rearing methods (Sheppard et al. 2002) and predict fitness characters of adult flies. The influence of parental environment on offspring development and the interaction between diet and temperature on development merit further study.

Acknowledgments

We thank W. C. Bridges and J. W. McCreadie for statistical advice and C. Geden, L. Higley, and K. Shoenly for comments on an earlier draft of the manuscript. This study was supported by National Integrated Water Quality Program Grant 2004-51130-02237.

References Cited

Adachi, I. 1994. Development and life cycle of *Anoplophora malasiaca* (Thomson) (Coleoptera: Cerambycidae) on citrus trees under fluctuating and constant temperature regimes. Appl. Entomol. Zool. 29: 485–497.

Alcock, J. 1990. A large male competitive advantage in a lekking fly, *Hermetia comstocki* Williston (Diptera: Stratiomyidae). Psyche 97: 267–279.

Amalraj, D. D., N. Sivagnaname, and P. K. Das. 2005. Effect of food on immature development, consumption rate, and relative growth rate of *Toxorhynchites splendens* (Diptera: Culicidae), a predator of container breeding mosquitoes. Mem. Inst. Oswaldo Cruz 100: 893–902.

Anderson, G. S. 2000. Minimum and maximum development rates of some forensically important Calliphoridae (Diptera). J. Forensic Sci. 45: 824–832.

Axtell, R. C., and J. J. Arends. 1990. Ecology and management of arthropod pests of poultry. Annu. Rev. Entomol. 35: 101–126.

Bondari, K., and D. C. Sheppard. 1981. Soldier fly larvae as feed in commercial fish production. Aquaculture 24: 103–109.

Booth, D. C., and C. Sheppard. 1984. Oviposition of the black soldier fly, *Hermetia illucens* (Diptera: Stratiomyidae): eggs, masses, timing, and site characteristics. Environ. Entomol. 13: 421–423.

Bradley, S. W., D. C. Booth, and D. C. Sheppard. 1984. Parasitism of the black soldier fly by *Trichopria* sp. (Hymenoptera: Diapriidae) in poultry houses. Environ. Entomol. 13: 451–454.

Byrd, J. H., and J. C. Allen. 2001. The development of the black blow fly, *Phormia regina* (Meigen). Forensic Sci. Int. 120: 79–88.

Byrd, J. H., and J. F. Butler. 1997. Effects of temperature on *Chrysomya rufifacies* (Diptera: Calliphoridae) development. J. Med. Entomol. 34: 353–358.

Clark, K., L. Evans, and R. Wall. 2006. Growth rates of the blowfly, *Lucilia sericata*, on different body tissue. Forensic Sci. Int. 156: 145–149.

De Haas, E. M., C. Wagner, A. A. Koelmans, M.H.S. Kraak, and W. Admiraal. 2006. Habitat selection by chironomid larvae: fast growth requires fast food. J. Anim. Ecol. 75: 148–155.

Furman, D. P., R. D. Young, and E. P. Catts. 1959. *Hermetia illucens* (Linnaeus) as a factor in the natural control of *Musca domestica* Linnaeus. J. Econ. Entomol. 52: 917–921.

Greenberg, B. 1991. Flies as forensic indicators. J. Med. Entomol. 28: 565–577.

Hogsette, J. A. 1992. New diets for production of house flies and stable flies (Diptera: Muscidae) in the laboratory. J. Econ. Entomol. 85: 2291–2294.

Hunter, M. D., and J. N. McNeil. 2000. Geographic and parental influences on diapause by a polyphagous insect herbivore. Agric. Forest Entomol. 2: 49–55.

Kamal, A. S. 1958. Comparative study of thirteen species of sarcosaprophagous Calliphoridae and Sarcophagidae (Diptera). I. Bionomics. Ann. Entomol. Soc. Am. 51: 261–270.

Kaneshrajah, G. and B. Turner. 2004. *Calliphora vicina* larvae grow at different rates on different body tissues. Int. J. Legal Med. 118: 242–244.

Keena, M. A. 2005. Pourable artificial diet for rearing *Anoplophora glabripennis* (Coleoptera: Cerambycidae) and methods to optimize larval survival and synchronize development. Ann. Entomol. Soc. Am. 98: 536–547.

Liu, Z. D., P. Y. Gong, K. J. Wu, and D. M. Li. 2004. Effects of parental exposure to high temperature on offspring performance in the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae): adaptive significance of the summer diapause. Appl. Entomol. Zool. 39: 373–379.

Lord, W. D., M. L. Goff, T. R. Adkins, and N. H. Haskell. 1994. The black soldier fly *Hermetia illucens* (Diptera: Stratiomyidae) as a potential measure of human postmortem interval: observations and case histories. J. Forensic Sci. 39: 215–222.

Minitab. 2007. Minitab release 15: statistical software for Windows. Minitab, State College, PA.

Newton, G. L., C. V. Booram, R. W. Barker, and O. M. Hale. 1977. Dried *Hermetia illucens* larvae meal as a supplement for swine. J. Anim. Sci. 44: 395–400.

Pujol-Luz, J. R., P. Abdon da Costa Francez, A. Ururahy-Rodrigues, and R. Constantino. 2008. The black soldier-fly, *Hermetia illucens* (Diptera, Stratiomyidae), used to estimate the postmortem interval in a case in Amapá State, Brazil. J. Forensic Sci. 53: 476–478.

Sheppard, D. C., G. L. Newton, and S. A. Thompson. 1994. A value added manure management system using the black soldier fly. Bioresource Technol. 50: 275–279.

Sheppard, D. C., J. K. Tomberlin, J. A. Joyce, B. C. Kiser, and S. M. Sumner. 2002. Rearing methods for the black soldier fly (Diptera: Stratiomyidae). J. Med. Entomol. 39: 695–698.

Tomberlin, J. K., and D. C. Sheppard. 2001. Lekking behavior of the black soldier fly, *Hermetia illucens* (Diptera: Stratiomyidae). Fla. Entomol. 84: 729–730.

Tomberlin, J. K., and D. C. Sheppard. 2002. Factors influencing mating and oviposition of black soldier flies (Diptera: Stratiomyidae) in a colony. J. Entomol. Sci. 37: 345–352.

Tomberlin, J. K., D. C. Sheppard, and J. A. Joyce. 2002. A comparison of selected life history traits of the black soldier fly (Diptera: Stratiomyidae) when reared on three diets. Ann. Entomol. Soc. Am. 95: 379–387.

Tomberlin, J. K., D. C. Sheppard, and J. A. Joyce. 2005. Black soldier fly (Diptera: Stratiomyidae) colonization of pig carrion in South Georgia. J. Forensic Sci. 50: 152–153.

Trudgill, D. L., A. Honek, D. Li, and N. M. Van Straalen. 2005. Thermal time-concepts and utility. Ann. Appl. Biol. 146: 1–14.

Received 22 December 2008; accepted 7 April 2009.