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The development of the black blow fly, *Phormia regina* (Meigen)

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Abstract

The black blow fly, *Phormia regina* (Meigen) is a primary species commonly utilized to indicate a postmortem interval, or more appropriately a ''time since colonization''. Due to the importance of this species as a secondary myiasis producer in livestock operations, and more recently as a time since death indicator in the field of forensic entomology, a considerable amount of data on its growth and development has been generated. However, the developmental time as reported by these studies varies greatly, and current more detailed data is needed for use in medicocriminal entomology. Hourly developmental data is presented under constant temperatures of 10, 15, 20, 25, 30, 35 and 40°C, and cyclic temperatures of 10–15, 15–25, 25–35 and 35–45°C. This study is in agreement with the results reported by Kamal [Comparative study of thirteen species of sarcosaprophagous Calliphoridae and Sarcophagidae (Diptera). I. Bionomics, Ann. Entomol. Soc. Am. 51 (1958) 261] and Melvin [Incubation period of eggs of certain musciod flies at different constant temperatures, Ann. Entomol. Soc. Am. 27 (1934) 406] only at temperatures of 25°C and below. Bishopp [Flies which cause myiasis in man and animals: some aspects of the problem, J. Econ. Entomol. 8 (1915) 317] reported a shorter developmental duration for larval stages than what was produced with our laboratory rearings.

Keywords: Black blow fly; Forensic entomology; Postmortem interval

1. Introduction

Historically, the black blow fly, *Phormia regina* (Meigen), has been reported as a secondary myiasis producer in both castration and dehorning operations throughout the southeastern US, and in sheep strike within the southwestern US [1–3]. It has also been reported that the larvae of this species have accounted for 67% of the larvae recovered from the wounds of domestic animals [4]. Although *P. regina* has been used in the past for maggot therapy, it has a propensity to invade healthy tissues [1,3,5]. Coffey [6] showed this species is also commonly attracted to the dung of humans and domestic animals. Currently this species is only a minor nuisance in livestock operations, but it is gaining a new-found importance in the field of forensic entomology as one of the primary species utilized to indicate the postmortem interval in human deaths throughout North America. The species biology and development of *P. regina* has been studied in detail [2,5,7,8–14]. However, the developmental time of *P. regina* reported in theses studies varies greatly, and in some instances is not presented with the detail needed for case analysis in medicocriminal entomology. Therefore, more detailed developmental data is needed for use in case analysis and to aid in resolving the discrepancies in past literature.

In North America, the major forensic importance of this species is due to *P. regina* being the dominant species in northern climates of the US during the summer months, as the more moderate maximum temperatures do not hamper its activity. Conversely, it is the dominant fly in the southern US during the winter months. Within the southern US, it is most commonly recovered from human remains during the winter months (October through March), with populations being reduced by high temperatures during the summer months. Although relatively tolerant of cold weather, Deonier [2] found that the activity of *P. regina* is inhibited when monthly temperatures averaged below 10°C. More recently, Haskell [15] found that adult activity is inhibited at only 12.5°C. This species of fly is not tolerant of hot conditions and does not survive the warm summers of the southern US [3,16].

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In many studies *P. regina* has comprised over 50% of the blow fly fauna [17,18]. In Texas, Cushing and Parish [9] reported a gradual increase in *P. regina* populations from September to a peak in April, after which populations rapidly decreased and became minimal in June. They showed that the population of *P. regina* fell rapidly with the higher temperatures of late April. However, Savage and Schoof [19] reported its peak abundance during June in Kansas, and Williams [20] described peak abundance from June through September in New York. Likewise, Denno and Cothran [10] state that *P. regina* was the most dominant species on carrion during the warm season in central California.

Since *P. regina* is very abundant in the southern US during the cooler months, and in northern US and Canada during the summer, this species will undoubtedly be recovered from variety of forensic investigations involving human remains. Recent descriptions of its development and life stage duration are not available in the current literature, and due to its tremendous forensic importance, a detailed study of its developmental duration under varying temperature regimes was undertaken.

2. Materials and methods

Adult and larval *P. regina* specimens were collected from human cadavers and from inverted cone traps baited with pork, chicken, and fermenting sunflower and millet seed. These adults were held in an insectary at 25 ± 2°C, 75–80% relative humidity, and a photoperiod of 14:10 (light (L):dark (D)). The F2 generation colonies used for this study were held in screened cages (54 cm × 28 cm × 28 cm) with 250 adult flies being fed a 50:50 mixture of table sugar and powdered milk, with fresh water supplied continuously.

2.1. Egg eclosion rate and duration

Eclosion data was determined for constant temperatures of 10, 15, 20, 25, 30, 35 and 40°C (±1°C). Cyclic temperature regimes of 10–15, 15–25, 25–35 and 35–45°C (±1°C) (12 h maximum/minimum cycle) and continuous lighting was also utilized in determining eclosion data. Observations were made every 30 min so that newly emerged larva could be counted and removed. The time of peak eclosion (mode), eclosion duration, and mean time was determined by exposing center cut lean pork to the gravid adult females within the colony cages for 20 min. For each of the three replications, pork was removed after this period and approximately 600 eggs were counted and placed into a petri dish held in a Percival® (Boone, IA) environmental chamber until hatching. The three experimental repetitions at each temperature regime were then consolidated and the peak eclosion rate, duration, and median time were plotted with Microsoft Excel.

2.2. Cyclic and constant temperature development

Larval growth was determined for constant temperatures between 10 and 40°C (±1°C) at 5°C increments, and cyclic temperature regimes of 10–15, 15–25, 25–35 and 35–45°C (±1°C). Such temperature cycles were selected to encompass the broadest range of temperatures feasible while remaining within the physical limitations of our test facility and labor requirements. All treatments had a photoperiod of 12:12 (L:D) (h) and 75% RH. The photoperiod of 12:12 (L:D) (h) was selected so that larval sampling would occur during the period shift. Adult flies utilized for colony maintenance purposes were allowed to develop at constant 25°C (±2°C) and 14:12 (L:D) cycle.

Three groups of 400 eggs (each <20 min old) were transferred into three S970 Dixie® cup (8.5 cm diameter, 11 cm high, James River, Norwalk, CT) containing 275 g of whole center-cut lean pork, and immediately were placed into a Percival® environmental chamber (Boone, IA) with ±1°C control. This procedure was repeated at 2 h intervals until six replicates were prepared, with a 12 h interval between the first and last of the six replicates. The ratio of 1.5 larvae per 1.0 g of pork was maintained by adding meat to the cups twice daily so that the metabolic heat generated by the feeding larvae would not be higher than the growth chamber settings and thereby accelerate growth rates. Although some larval aggregations were noticed, a type-K thermocouple fluid probe inserted in each rearing cup recorded no significant temperature elevations of the rearing media.

Six maggots randomly selected from within each of the three subsamples, were removed twice daily (for a total of 108 larvae removed from the entire sample population at 12 h intervals). Sampling continued until 50% of the cohort had pupated. The parameters for the time of pupation was determined by failure of the larvae to elongate and move in response to being disturbed [21]. The mean lengths of the sample larvae were plotted in line graph format using Microsoft Excel.

For measurement purposes, maggots were killed immediately in boiling water and transferred to 75% ethyl alcohol. It should be noted that this technique will fully extend the larval body and may not be consistent with results obtained from larvae preserved in other solutions. The body length of the preserved larvae was measured to the nearest 0.1 mm using an electronic digital caliper. Selection of this sampling method was chosen because of the common practice of collecting a representative sample of the insect fauna and then also selecting for the largest maggots at a death scene. In doing so, two samples are created, one random sample of the larvae present, and the other selected for the largest individuals. When selecting for the largest specimens, the entomologist usually assumes that the largest larvae of a particular species are the oldest individuals and likely developed from the first egg clutch deposited on the body. This fact may or may not be true, and must

be determined by on a case by case basis by the forensic entomologist.

Adult emergence rates were determined by rearing cohorts of larvae and containing the pupae in clear emergence traps (BioQuip Corporation) under temperatures of 10, 15, 20, 25, 30, 35 and 40°C (±1°C). Cyclic temperature regimes of 15–25, 25–35 and 35–45°C (±1°C) (±12 h maximum/minimum cycle) were also utilized to obtain adult emergence data. Constant lighting (835 lx) was used for all temperature regimes to avoid the possibility of photoperiod dependent emergence gating. At the onset of adult emergence, observations were made at half-hour intervals so that the teneral adults could be counted and removed from the emergence trap. Three experimental replications were conducted at each temperature regime and plotted with Microsoft Excel before being consolidated to determine the mean eclosion rate.

3. Results

The cyclic temperature regimes produced onset of egg eclosion ranging from 7 to 18 h with an overall duration of 5–12 h. Onset of eclosion had occurred within 24 h of oviposition under all cyclic regimes with peak eclosion occurring in as little as 8.5 h (Table 1). Under constant temperatures, onset of egg eclosion ranged from a minimum of 8 h at 40°C to 32 h at 15°C. Completion of eclosion required over 100 h at 15°C. Peak eclosion rates ranged from 10 to 68 h (Table 2). The 40°C temperature range produced a minimum duration of 5 h, and the peak hatch rate occurred only 10 h after oviposition (Fig. 1). All eggs hatched 14 h after oviposition at 40°C. No egg hatch was observed with the 10°C temperature regime, and eclosion during the 15°C temperature regime produced the longest eclosion duration of between 32 and 116 h, with peak hatch occurring at 68 h (Fig. 2). Cyclical conditions of 25–35°C delayed onset of eclosion by only 1 h, and prolonged the duration by 0.5 h when compared to a constant 30°C (Fig. 3), however, this difference was not statistically significant.

Incremental increases in the constant temperature regimes produced a consistently shorter time for stage onset and shorter stadium duration in this species with the exception of the first instar at the 30 and 35°C regime, and the pupal stage at 35°C. The constant temperature regime studies produced the first instar larvae from as little as 8–32 h, and the pupa from 98 to 389 h (Table 3). In the 40°C regime, development occurred normally until larvae reached the migratory (or prepupal) stage. Once in this stage, larval mortality increased with pupae forming at 128 h. However, the majority of the migratory larvae failed to develop further and quickly desiccated and died under the high temperature regimes. Normal development resumed at the lower temperature regime of 35°C.

With the 35°C constant temperature regime, the first instar was recovered within 8–16 h after oviposition, which agreed with the range previously established by Melvin [14] for egg eclosion at that temperature. As with the 35–45°C regime, development of the larvae throughout the early third instar proceeded normally and the majority of the sample population entered the prepupal stage successfully after 110 h (Fig. 4A). However, only 13% of those larvae underwent successful pupation, and no adults emerged from the pupal stage (Table 4). Normal development (successful from egg through adult emergence), resumed under lower temperature constant conditions of 35°C (Fig. 4B). Pupation was delayed by 16–52 h in the 30°C regime when compared to the 35 and 25°C cycle (Fig. 5A and B). The 25°C repetition produced the shortest prepupal period of all

Table 1
Cyclic temperature egg eclosion data for *Phormia regina*

Temperature (°C)	Peak eclosion (mode) (h)	Range (h)	Mean (h)	S.D. (h)
45–35	8.5	7–12	9.1	0.9
35–25	12	10–22	17.9	1.1
25–15	22	18–30	21.5	0.7

Table 2
Constant temperature egg eclosion data *Phormia regina*

Temperature (°C)	Peak eclosion (mode) (h)	Range (h)	Mean (h)	S.D. (h)
40	10.0	8–13	9.8	0.9
35	15.5	12–18.5	15.7	0.9
30	17.5	15–20.5	17.4	0.8
25	19.0	16.5–22	18.9	0.8
20	20.5	19–25	21.2	1.2
15	68.0	30–116	70.3	17.4
10	–	–	–	–

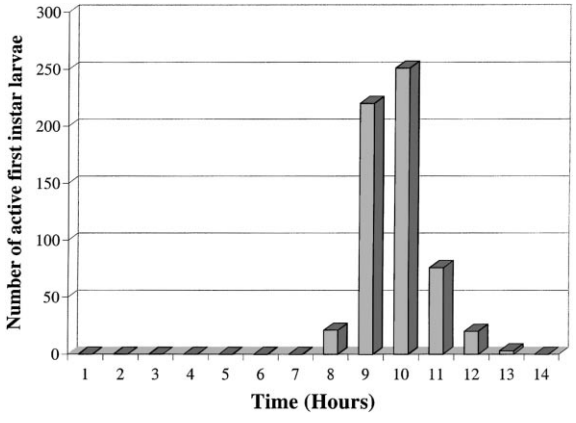

Fig. 1. Eclosion of *Phormia regina* eggs under 40°C (±1°C) constant temperature.

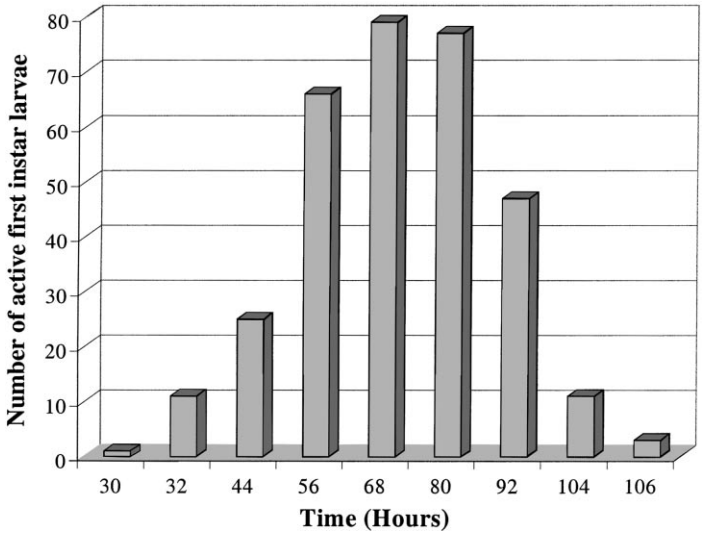

Fig. 2. Eclosion of *Phormia regina* eggs under 15°C (±1°C) constant temperature.

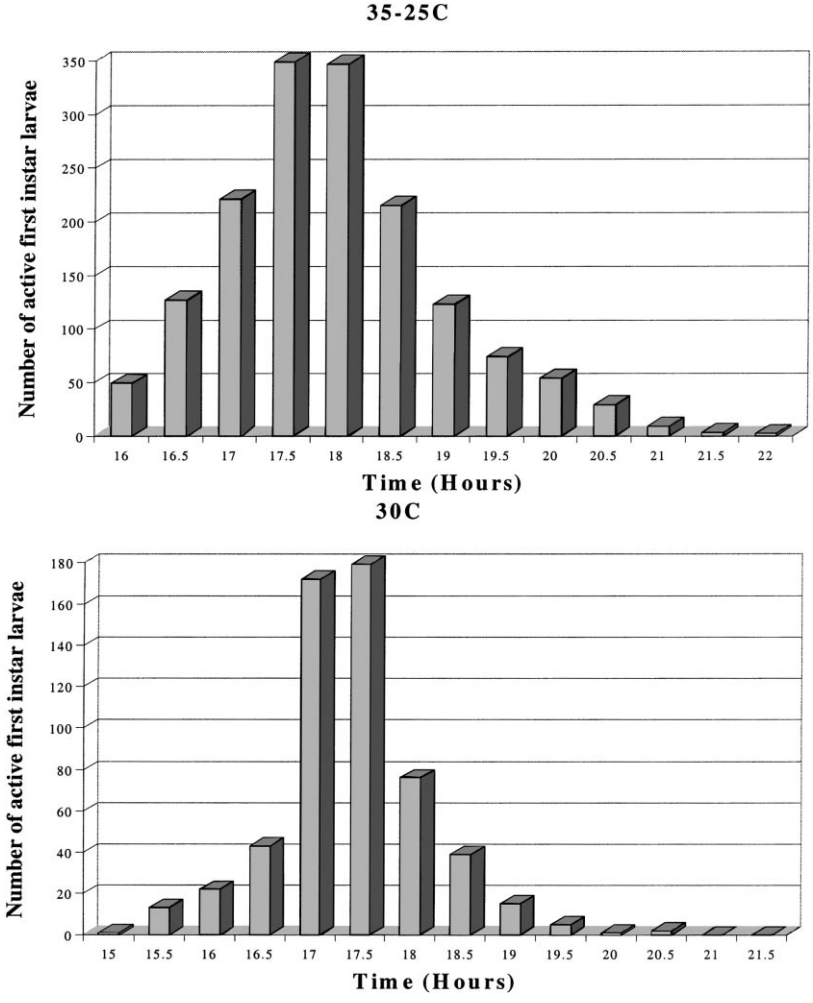

Fig. 3. Comparison of *Phormia regina* egg eclosion rates between 25 and 35°C (±1°C) cyclical temperature regime and 30°C (±1°C) constant temperature.

Table 3
Constant temperature stadia data (in h) for the immature stages of *Phormia regina*

Temperature (°C)	First instar (mean ± S.D.)	Second instar (mean ± S.D.)	Third instar (mean ± S.D.)	Prepupa (mean ± S.D.)	Pupa (mean ± S.D.)
40	8–16 (12 ± 2)	10–36 (23 ± 7)	32–88 (60 ± 14)	110–165 (146 ± 26)	128 + no emergence
35	12–20 (16 ± 2)	14–48 (31 ± 9)	36–96 (66 ± 15)	76–148 (112 ± 18)	98–198 (148 ± 25)
30	12–24 (18 ± 3)	22–56 (39 ± 9)	50–142 (96 ± 23)	102–194 (148 ± 23)	150–266 (208 ± 29)
25	18–28 (25 ± 4)	26–62 (44 ± 9)	58–132 (95 ± 19)	122–190 (156 ± 17)	134–284 (209 ± 38)
20	19–40 (30 ± 5)	36–74 (55 ± 10)	62–102 (82 ± 10)	80–194 (192 ± 28)	188–300 (244 ± 28)
15	32–118 (75 ± 22)	80–190 (135 ± 28)	164–272 (218 ± 27)	288–422 (355 ± 33)	389–526 (458 ± 35)
10	–	–	–	–	–

constant temperatures that lasted only 68 h, with pupation of 50% of the sample population at 140 h (Fig. 5B). Growth curves at 20 and 15°C for this species displayed similar shapes with a progressively longer duration as temperature decreased. For these regimes, variability in larval length was greatest immediately before onset of the migratory or post-feeding stage (Fig. 6A and B).

A general trend for this species was that development under the cyclic temperature regimes was prolonged when compared with constant temperature conditions (Table 5) of

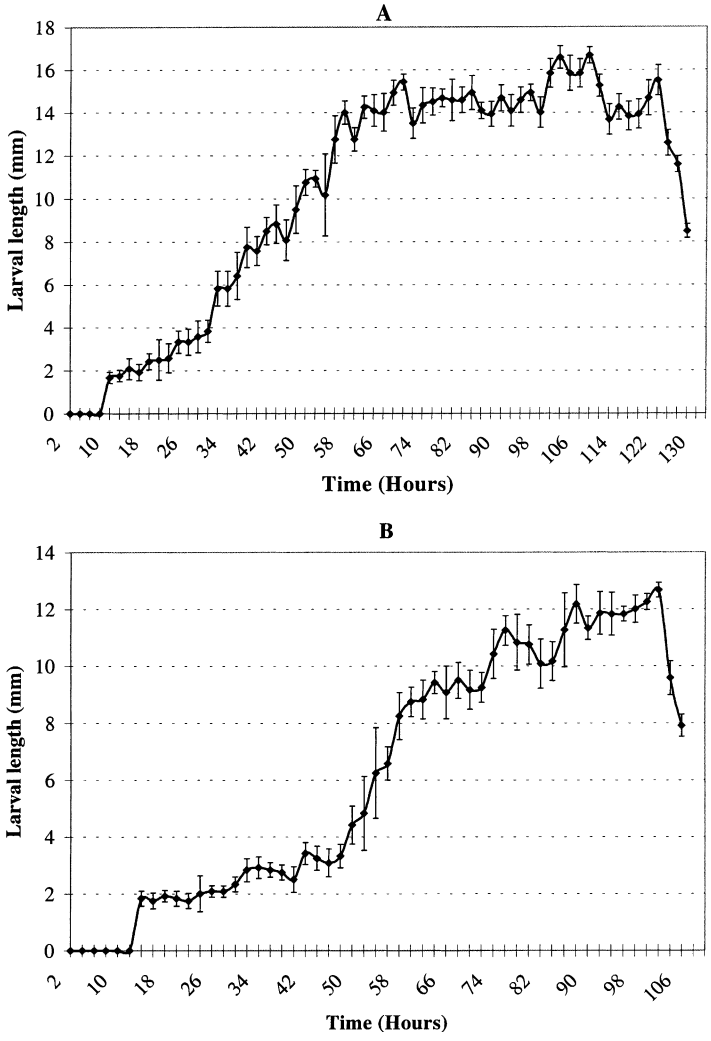

Fig. 4. Larval growth of *Phormia regina* under constant temperatures: A, 40°C (±1°C); B, 35°C (±1°C).

Table 4
Phormia regina larvae, pupae, and adults reaching described stage of development at 40 ± 10°C shown as a percentage of total population

Repetition	Migrating larvae	Pupae	Adults
1	16	6	0
2	7	6	0
3	18	2	0
4	6	6	0
5	13	11	0
Average (%)	12	6	0

the same mean. These results were consistent with the findings of Greenberg [12]. All larval instars grew normally under the 35–45°C regime and the majority of the sample population entered the prepupal stage (active migration away from food substrate) at 208 h (Fig. 7A). Only 40 h later, 4% of the prepupal larvae had pupated normally, and no adult emergence was ever observed under the 35–45°C temperature regime (Table 6).

Normal pupation patterns and adult emergence resumed under the cooler 25–35°C temperature cycle (Fig. 7B). Of the cyclic temperatures utilized, the 25–35°C regime produced the shortest prepupal period, which lasted only 42 h before the first 50% of the sample population pupated. Of the cyclic temperature regimes, the 15–25°C regime produced the longest larval duration of 420 h before 50% of the sample population had successfully undergone pupariation (Fig. 8). Complete development was not successful under cyclic conditions of 10–15°C.

Onset of adult emergence under the cyclic temperature regimes utilized in this study ranged from 352 to 532 h with a duration of 111 and 120 h, respectively. Adult emergence was complete by 652 h under the cyclic conditions of 15–25°C (Table 7). Development was not successful with the 35–45°C regime. The constant temperatures used in this study produced onset of adult emergence ranging from 212 to 672 h (Table 8), with an average duration of 149 h. The

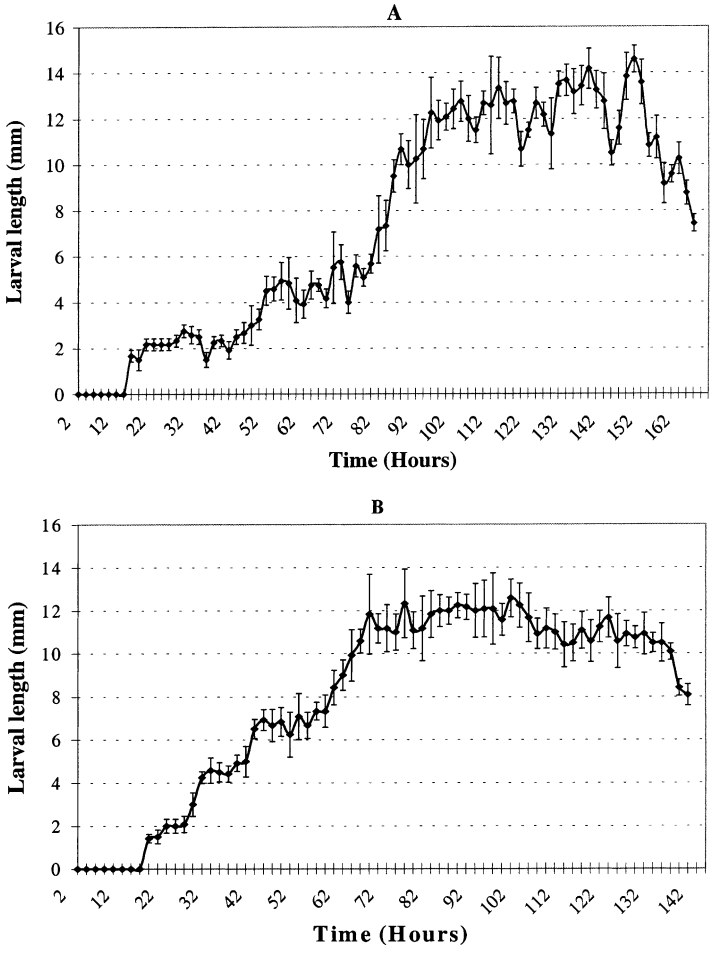

Fig. 5. Larval growth of *Phormia regina* under constant temperatures: A, 30°C (±1°C); B, 25°C (±1°C).

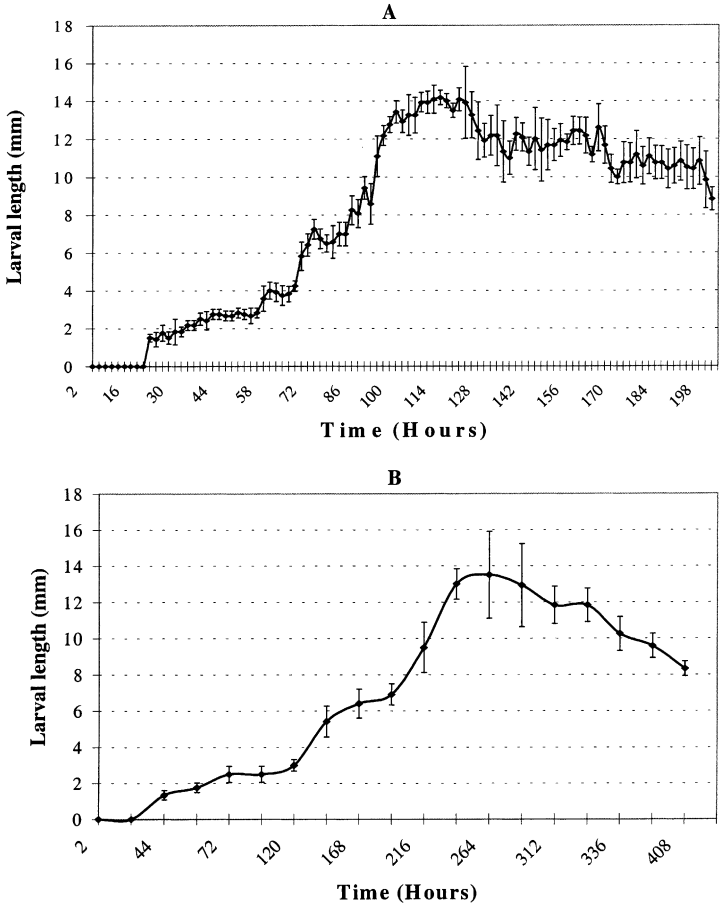

Fig. 6. Larval growth of *Phormia regina* under constant temperatures: A, 20°C (±1°C); B, 15°C (±1°C).

shortest duration that was required for completion of adult emergence was 108 h at 35°C. Adult emergence did not occur with the 35–45°C regime or during a constant temperature of either 40 or 10°C.

4. Discussion

The most extensive treatment on the egg hatch time of *P. regina* was that undertaken by Melvin [14]. At 40°C Melvin reported hatch in 8.7 h, with no hatch occurring a slightly higher regime of 43°C. In this study, a constant temperature of 40°C produced onset of egg eclosion ranging from 8 to 13 h with peak eclosion occurring 10 h from oviposition. Results such as these are in agreement with the studies conducted by Melvin [14]. The 35–45°C cyclic regime with peak eclosion only 8.5 h after oviposition also compares very well with the 8.7 h reported by Melvin [14].

The egg hatch times reported by Kamal [13] at a constant temperature of 26.7°C has a range of 10–22 h, and is essentially the same range reported in this study. Additionally, the peak emergence reported in this study occurred in 19 h at 25°C, and in 15.5 h at 30°C (compared with 16 h in Kamal's study). At temperatures of 30°C and above, Melvin's [14]

Table 5
Cyclic temperature stadia data (in h) for the immature stages of *Phormia regina*

Temperature (°C)	First instar (mean ± S.D.)	Second instar (mean ± S.D.)	Third instar (mean ± S.D.)	Prepupa (mean ± S.D.)	Pupa (mean ± S.D.)
45–35	7–22 (15 ± 4)	13–36 (25 ± 6)	30–204 (117 ± 44)	208–258 (233 ± 26)	248 + no emergence
35–25	14–20 (17 ± 2)	18–42 (30 ± 6)	38–184 (113 ± 37)	158–200 (179 ± 11)	194–428 (311 ± 59)
25–15	24–46 (35 ± 6)	40–92 (66 ± 13)	80–384 (232 ± 76)	276–396 (336 ± 30)	336–478 (407 ± 36)

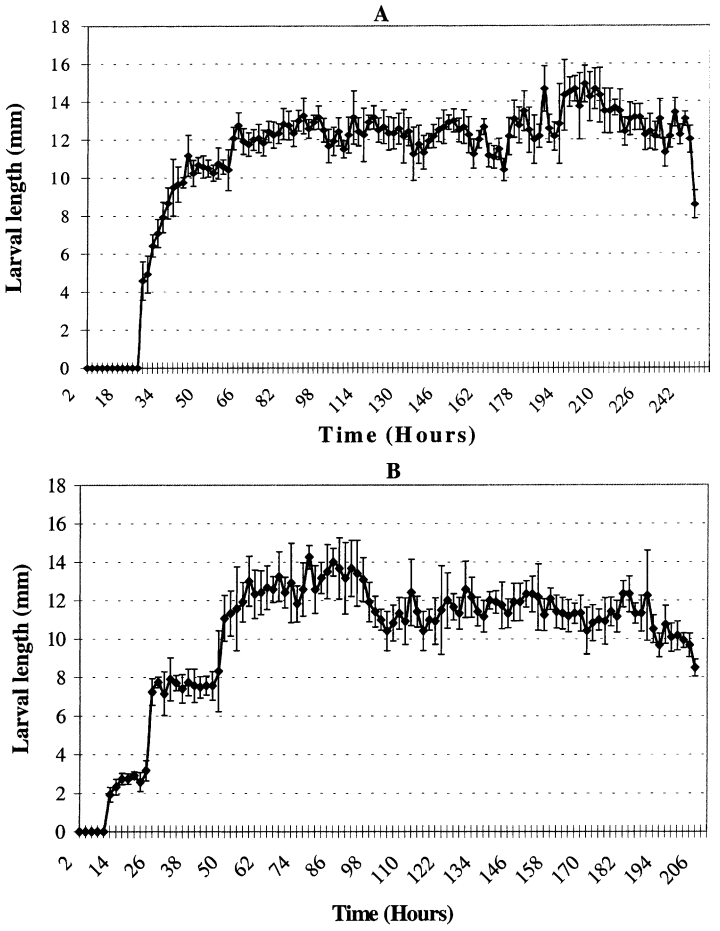

Fig. 7. Larval growth of *Phormia regina* under cyclic temperature: A, 35–45°C (±1°C); B, 25–35°C (±1°C).

developmental study reported shorter developmental duration than found here. However, at 25°C and below, his data fell within the ranges reported in this study. Both Melvin [14] and the finding of this study indicate that 40°C approaches the upper lethal temperature limit for the egg stage.

One of the most detailed descriptions of *P. regina* larval development is by Kamal [13], who reported a first instar duration with a range of 11–32 h at 27°C. This was a shorter developmental period than either our 30 or 25°C regime, with the onset of the first instar at 12 and 18 h, respectively. Onset of the migrating, or postfeeding, stage was clearly

Table 6
Number of *Phormia regina* larvae, pupae, and adults reaching described stage of development at 35–45°C (±1°C) shown as a percentage of total population

Repetition	Migrating larvae	Pupae	Adults
1	1	0.7	0
2	8	9	0
3	3	3	0
4	6	6	0
5	3	3	0
Average (%)	4	4	0

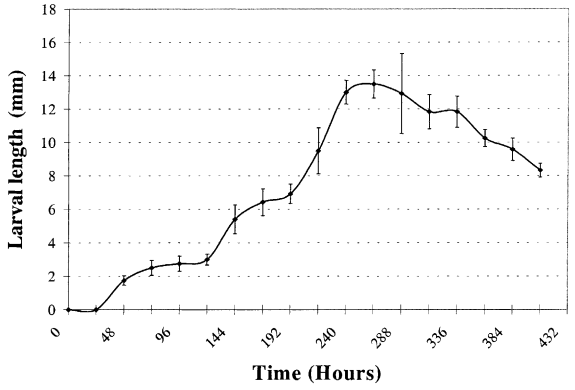

Fig. 8. Larval growth of *Phormia regina* under cyclic temperature regime 15–25°C (±1°C).

Table 7
Cyclic temperature adult emergence data for *Phormia regina*

Temperature (°C)	Peak emergence (mode) (h)	Range (h)	Mean (h)	S.D. (h)
45–35	–	–	–	–
35–25	374	352–463	403	28
25–15	580	532–652	570	31

indicated by the larvae actively moving away from the food substrate and by a marked reduction in body length as well as a noticeable color change.

Kamal [13] reported a pupal duration of 96–261.6 h, while the 30 and 25°C regime used in this study produced a pupal stage of 187 and 151 h, respectively. Although the duration reported in this study falls within the range established by Kamal [13], it disagrees with Bishopp's [7] study which reported a pupal period in as short as 72 h. The shortest pupal duration reported here was 100 h under constant conditions of 35°C. This study produced oviposition and subsequent larval development at both 20 and 15°C. However, no oviposition or development occurred at 10°C.

Bishopp [7], James [3], and Kamal [13] reported that the egg to adult interval could be as short as 10 days. In this project the first adults emerged in as little as 8.8 days at 35°C, however, the mean time of adult emergence was 11 days at this temperature. The developmental duration appeared to be adversely affected at temperatures above 35°C, with mortality increasing dramatically until no adult emergence occurred at 40°C. Adult emergence under all temperature regimes was unimodal.

P. regina was easily kept in laboratory colony although the adults appeared to frighten easily and suffered more wing and leg damage from impacting with the sides of the cage than did other species kept in colony for this work. Adults survived well under varying population densities and tolerated overcrowding with no observed adverse effects such as increased mortality. The larval colony thrived on a diet of lean pork, however, if the food supply became depleted, the larvae quickly dispersed. Once this dispersal behavior commenced, many larvae would not resume normal feeding when placed on a replenished food supply. This could be from the fact that the depleted food supply triggered larval physiology into a premature migration phase. Although this behavior needs to be more thoroughly investigated, it should be noted and considered when shipping or transporting larvae to a qualified forensic entomologist for case analysis.

Table 8
Constant temperature adult emergence data for *Phormia regina*

Temperature (°C)	Peak emergence (mode) (h)	Range (h)	Mean (h)	S.D. (h)
40	–	–	–	–
35	248	212–320	265	27
30	286	238–358	289	30
25	324	264–444	342	45
20	454	358–526	434	34
15	792	672–840	752	51
10	–	–	–	–

This study is in agreement with portions of the results of Bishopp [7], James [3], and Kamal [13]. However, variations do exist between this study and those of Kamal [13] and Melvin [14] at temperatures above 25°C, and those differences become more pronounced as environmental temperature approaches the upper lethal temperature threshold. Additionally, Melvin [14] reported a shorter development duration for the larval stages of this species. It is obvious that the forensic entomologist must be cautious when applying growth and development data of this species to criminal and civil investigations when environmental temperatures are 25°C or above. Armed with such knowledge and more refined temperatures and development data, the investigation will be better prepared to estimate the postmortem interval based on the development of *P. regina* when it is recovered as entomological evidence from the death scene.

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