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ORIGINAL ARTICLE

Effects of population variations and temperature on *Chrysomya megacephala* (Diptera: Calliphoridae) development: implications for estimating the postmortem interval

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Abstract

Forensic entomology requires knowledge of the developmental rates of the species that colonize a body after death to estimate the postmortem interval (PMI). These developmental rates may vary depending not only on the species but also on the geographic location due to population differences. Therefore, the objectives of this work were to determine the developmental duration of the forensically important fly *Chrysomya megacephala* under constant controlled and field condition temperatures and to compare these results, through a meta-analysis, with data reported by other authors on populations from different localities. For this, *C. megacephala* colonies were established in the laboratory, and the duration of the life cycle was studied at two controlled temperatures (25 °C and 27 °C) and field conditions (27.5 ± 3.2 °C). Analysis of variance was performed to determine differences in developmental time and larval length between constant laboratory temperatures and field conditions. A generalized linear model was performed with predictor variables extracted from the literature (diet, relative humidity, latitude, longitude) to evaluate the effect of population variation on developmental times. The results showed significant differences in developmental times between 25 and 27 °C. As expected, the complete life cycle of *C. megacephala* was shorter at 27 °C. Finally, the meta-analysis suggested differences between the developmental times of different populations, based on temperature and geographic location. The results of this study provide fundamental developmental data to use *C. megacephala* in PMI estimations. Finally, we suggest that, when making expert reports, information from local populations should be used to determine a more accurate and reliable PMI.

Keywords Forensic entomology · Life cycle · PMI · Meta-analysis · Geographic location

Introduction

The estimation of the postmortem interval (PMI), defined as the time elapsed between death and the finding of the corpse, is a crucial step in a death scene investigation [1]. Knowledge of this time helps to reconstruct the events, determine the circumstances of death, link or rule out suspects, or reinforce the witnesses' testimony [2]. Legal medicine estimates the PMI by using different techniques based on postmortem changes in soft tissue during the first hours after death, such as the drop in body temperature, the presence of lividity, and cadaveric rigidity [3]. However, when corpses initiate the bloating stage, estimates based on pathological criteria become more complex and less accurate [1]. In times of high temperatures, this stage can be established from 72 h after death [4, 5]. In these cases, another discipline such as entomology is necessary to aid in estimations with more appropriate techniques [6–9].

Forensic entomology studies the insects and other arthropods that arrive on a dead body [10]. The colonization of the corpse by necrophagous insects starts a few minutes after death, following a predictable sequence. Therefore, the PMI can be estimated using two methods: insect succession and age estimation. Insect succession involves ecological succession and is based on the known arrival sequence of

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entomofauna in a decomposing body [10–12], whereas age estimation is based on the determination of the age of the different developmental stages of insects, especially considering the oldest individuals [13]. In general, the succession method is used when the corpse has been dead for between a month and a year or more, with the estimated window of death broadening as time since death increases. Instead, the age estimation method is used when death occurred less than a month prior to the finding of the corpse and can give a narrower and more precise time interval. Using available information on the development of insects of forensic interest, and temperature data, it is possible to calculate the age of the immature individuals in the corpse and thus estimate the time when the insects initially colonized it [14, 15].

Since insects are unable to regulate their internal body temperature (i.e., they are ectotherms), environmental temperatures strongly alter their metabolism, directly affecting the developmental rates of their life cycles [16]. In this way, the time required to complete their life cycle depends on the physiology of each species and the environmental temperature conditions. Likewise, certain species may present local adaptations depending on the environmental conditions of the locality they inhabit, which leads them to develop physiological, morphological, and behavioral mechanisms that may provide them an advantage in their habitat [17–19]. For example, in Austria, Grassberger and Reiter [20] observed that, at 28 °C, the duration of the life cycle of the forensically important fly *Lucilia sericata* was 12 days, whereas, in the USA, Roe and Higley et al. [21] found that the life cycle of this same species at the same temperature lasted 8 days, and in Ecuador, Pruna et al. [22] found that it lasted 16 days. This is of great importance at the time of estimating the PMI in a criminal investigation since incorrect insect biological information would lead to wrong conclusions.

The most important necrophagous insects used during forensic investigations are blowflies (Diptera: Calliphoridae). Species of this family are usually common, highly abundant, and the first colonizers of a corpse [6]. Among blowflies, the oriental latrine fly *Chrysomya megacephala* (Fabricius 1974) is commonly found in cadavers in many parts of the world [23–26]. This species, native to the Oriental and Australasian regions, has rapidly spread through Africa [27, 28] and the New World [24]. Currently, this species is widely distributed throughout the American continent [29], from North America [23], passing through Central America [30] to South America [31–34] and the Caribbean islands [35, 36]. The reputation of *C. megacephala* as an early and dominant colonizer of carrion makes it a particularly attractive species to estimate the PMI [24, 37–39].

Since one of the methods to estimate the PMI requires knowing the life cycle of the entomological species collected from corpses and because insect development depends directly on the thermal conditions, the objective of this work was to determine the developmental duration of *C. megacephala* under two constant laboratory temperatures (25 °C and 27 °C) and field condition temperatures (27.5 ± 3.2 °C), in the city of Tapachula in Mexico. We also compared, through a meta-analysis, developmental rates between different populations of *C. megacephala* worldwide distributed.

Material and methods

Establishment of the colony and collection of eggs

The study was carried out in the facilities of the Centro Regional de Investigación en Salud Pública of the Instituto Nacional de Salud Pública (CRISP/INSP), located in Tapachula, Chiapas, Mexico (14.9N, 92.3W) during April 2018. Tapachula is characterized by the presence of a large variety of tree and bush species, among which *Mangifera indica*, *Theobroma cacao*, and *Coffea* sp. predominate. The region typically experiences a dry season from December to May and a rainy season from June to November (an average of 2500 mm over the season) and has a mean annual temperature of 27.1 °C (with a minimum and maximum of 22.5 °C and 31.4 °C respectively), and an altitude of 177 m.

Adults of *C. megacephala* were collected using traps baited with beef liver. In the laboratory, specimens were placed individually in transparent tubes for ocular observation and identified using Whitworth's taxonomic key [40]. The flies were then placed in 300-cm^3 cages held under laboratory conditions (controlled temperature of 25 °C and a not controlled mean relative humidity (RH) of 72%) and provided with water and a 50:50 mixture of sugar and powdered milk ad libitum. To obtain eggs, 100 g of beef liver was provided as oviposition substrate. All the eggs were collected the same day within 1 h after deposition from the F1 and F2 generations and then used throughout the study.

Experimental designs

In order to know the developmental time of each of the instar and pupa stages of *C. megacephala*, we conducted experiments under two different scenarios: two laboratory-controlled temperatures (25 °C and 27 °C, with 72% RH and a photoperiod of 12:12) and field conditions (27.5 ± 3.2 °C). We refer to field conditions as the exposure of specimens to fluctuating outdoor temperatures. A total of 100 eggs of *C. megacephala* were placed in each of 30 transparent plastic containers of 500 ml capacity, together with 200 g of vermiculite and 200 g of beef liver. Ten containers were used for each of the three temperature assays. The containers were protected with fine mesh cloth fastened with an elastic band. Containers for the field assays were exposed to environmental conditions but were kept inside a mesh cage (1 m × 1 m)

and under a roof to prevent invasion by other scavengers and to protect them from the rain. The temperature and RH percentages were recorded every hour with a data logger Omega (Mod: OM-EL-USB-2-LCD-PLUS).

Eggs were monitored visually in person every hour, both during daytime and nighttime, until hatching was observed. After hatching, observations and larval sampling were performed every 12 h. Five larvae were randomly sampled from each of the 10 containers for every time point and temperature condition evaluated. The larvae were killed by immersing in hot water (80–90 °C) for 5 s to prevent shrinkage and then dried with a paper towel before taking measurements. Photographs of each larva were taken on a millimeter scale with the help of a 3.2 Mpx AmScope digital camera and an AmScope SM-4TZZ-144A-3 M tri-ocular stereomicroscope. The images were processed with the ImageJ software [41] to calculate the length of each larva. The larval instar of each specimen was also recorded at each observation based on their posterior spiracular slits. At the pupal stage, no samples were taken, and no measurements or any type of manipulation of the individual were performed. However, the observations continued every 12 h, to record the time of emergence of adults. The same procedure was carried out for the two controlled temperatures and the field assays.

Meta-analysis

A systematic bibliographic search was carried out to analyze the possible effects of population variations on developmental time by comparing different *C. megacephala* populations from different worldwide locations. The database was built from online searches on Google Scholar, Scielo, Science Direct, PubMed, Scopus, and Web of Science platforms, using the keywords "*Chrysomya megacephala*," "development," "life cycle," "life table," "stage," "temperature," "growth," and its relevant combinations. Only publications that included constant temperatures, geographic location, and all developmental stages (from eggs to adults) were used for records.

Data analysis

To determine differences in developmental times and larval lengths, an analysis of variance (ANOVA) was performed between temperatures (25 °C, 27 °C, and field conditions) followed by Tukey's post-hoc test. To assess differences between the developmental times of different populations recorded by other authors around the world, we fitted generalized linear models (GLMs) with Poisson error structure with a log link function (glm function in the R base package). Models included both the temperature and RH as numerical predictors, the diet (food source used to culture the larvae) as a categorical predictor (with four categories: beef meat, pork meat, liver, and lamb meat), the latitude and the longitude (decimal degrees) as numerical predictors, and the interactions between latitude and longitude as the geographic location of localities [42–44] (Table 1). Latitude values were used as distance from the equator independently of whether the study region was located in the northern or southern hemisphere. The developmental time was the dependent variable. Analyses were performed using the R statistical environment [45]. The minimum adequate model was selected using Akaike's information criterion (AIC).

Table 1 Variables used to fit generalized linear models for the developmental time of different *C. megacephala* populations

Locality	RH %	Temp °C	Lat	Long	Food source	Source
Seberang Penai	70	30	5.4 N	100.5 E	Beef meat	[38]
Chongqing	70	16, 19, 22, 25, 31, 34	29.5 N	106.5 E	Beef meat	[39]
Kerala	85	25	8.5 N	76.9 E	Beef meat	[48]
Brisbane	-	28	27.4 S	153 E	Beef meat	[49]
Bangalore	-	27	12.9 N	77.6 E	Liver	[50]
Giza	65	26	29.9 N	32.1 E	Beef meat	[51]
Punjab	-	22.7, 25, 28, 30	31.2 N	74.3 E	Lamb	[52]
Recife	75	26	8.0 S	34.8 W	Beef meat	[53]
Valencia	47	28	10.1 N	68 W	Liver	[54]
Aurangabad	19	10	19.8 N	75.3 E	Liver	[55]
Jacksonville	60	15, 20, 25, 30, 35	30.3 N	81.6 W	Liver	[56]
Suzhou	75	16, 19, 22, 25, 28, 31, 34	31.3 N	120.6 E	Pork meat	[57]
Kandy	70	20, 25, 27, 38	7.2 N	80.6 E	Beef meat	[58]
Kuala Lumpur	80	27, 30, 33	3.1 N	101.7 E	Liver	[59]
Tapachula	72	25, 27	14.9 N	92.3 W	Liver	Present study

Table 2 Mean developmental time (hours ± SD) of each instar of *C. megacephala* reared at two constant temperatures (25 °C and 27 °C) and under field condition temperatures (27.5± 3.2°C)

Temp °C	Condition	Hours (± SD)					
		Eggs	First instar	Second instar	Third instar	Pupa	Total
25	Lab	15 ± 0.6^{a}	32 ± 7^{a}	20 ± 7^{a}	60 ± 0^{a}	104 ± 14^{a}	231 ± 21^{a}
27	Lab	13 ± 0^{b}	24 ± 0^{b}	12 ± 0^{b}	60 ± 0^{a}	88 ± 7^{b}	197 ± 7^{b}
27.5 ± 3.2	Field	12 ± 0^{c}	24 ± 0^{b}	12 ± 0^{b}	48 ± 0^{b}	96 ± 0^{c}	192 ± 0^{b}

Different letters in the same column indicate statistically significant differences (Tukey's test, $p < 0.05$)

Table 3 Mean accumulated degree hours (ADH ± SD) of each instar of *C. megacephala* reared at two constant temperatures (25 °C and 27 °C) and under field condition temperatures (27.5 ± 3.2 °C)

Temp °C	Condition	ADH (± SD)					
		Eggs	First instar	Second instar	Third instar	Pupa	Total
25	Lab	375 ± 15^{a}	800 ± 173^{a}	500 ± 175^{a}	1500 ± 0^{a}	2600 ± 350^{a}	5775 ± 525^{a}
27	Lab	351 ± 0^{b}	648 ± 0^{b}	324 ± 0^{b}	1620 ± 0^{a}	2376 ± 189^{b}	5319 ± 189^{b}
27.5 ± 3.2	Field	330 ± 0^{c}	660 ± 0^{b}	330 ± 0^{b}	1320 ± 0^{b}	2640 ± 0^{c}	5280.2 ± 0^{b}

Different letters in the same column indicate statistically significant differences (Tukey's test, $p < 0.05$)

Results

The data logger recorded hourly temperature and RH data of assays under field conditions. RH was 76.6 ± 11% on average, ranging between 51.5 and 91.9%. Regarding temperature, the minimum and maximum recorded were 22.4 °C and 34.1 °C respectively, being 27.5 ± 3.2 °C on average.

With respect to the complete developmental time of *C. megacephala* (from egg to adult emergence), significant differences were found between growth at the two constant temperatures evaluated: 25 °C and 27 °C ($F = 29$; df = 2; Tukey's test, $p < 0.05$). The complete life cycle of *C. megacephala* was shorter at 25 °C than that at 27 °C, and also shorter at 25 °C than that at field condition temperatures (Tukey's test, $p < 0.05$) (Table 2). No differences were observed between 27 °C and field conditions (Tukey's test, $p = 0.999$). In addition, the developmental time of each stage also depended on the exposure temperature (Table 2). The data were expressed both in hours and in accumulated degree hours (ADH) (Tables 2 and 3) because both are widely used for the estimation of the PMI [46, 47].

The comparison between the two laboratory temperatures and the field condition temperatures showed differences in the percent time spent by *C. megacephala* at each instar and other developmental stages (df = 8, $F = 61$, $p < 0.05$) (Fig. 1). In particular, no differences were observed between stages L1 ($p = 0.999$) and L2 ($p = 0.999$) at 27 °C and field conditions or between L3 at 25 °C and L3 at 27 °C ($p = 1$). Although the field condition temperatures were similar to the higher controlled temperature evaluated (27 °C), the field temperatures recorded during each stage were different. For example, during stages L2 and L3, the mean temperature in the field was greater than 28 °C (Fig. 1).

Concerning larval size, significant differences in mean length were found between 25 and 27 °C (Tukey's test, $p < 0.05$) but not between field conditions and the two controlled temperatures evaluated (Tukey's test, $p = 0.692$ and $p = 0.883$ respectively; Fig. 2). No differences were found when analyzing the effect of temperature on the mean length of the different instars (df = 4, F = 0.8, $p = 0.5$; Table 4).

Meta-analysis

In our meta-analysis, we found 14 publications that had examined the development of *C. megacephala* populations from different locations at different temperatures that included all the stages of the cycle and detailed the

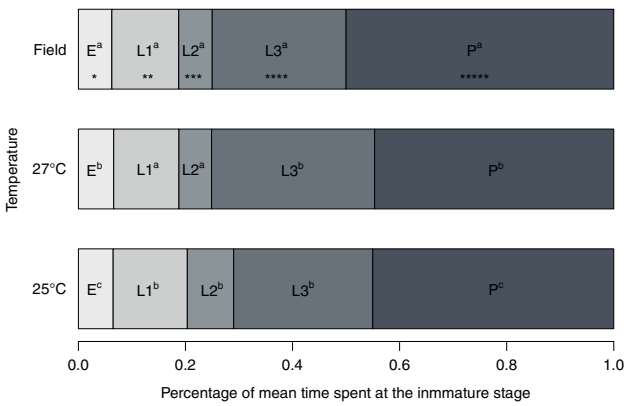

Fig. 1 Percentage of mean time spent by *C. megacephala* at each instar of development at two constant temperatures (25 °C and 27 °C) and field condition temperatures (27.5 ± 3.2 °C). Different letters in the same instar indicate statistically significant differences (Tukey's test, $p < 0.05$). Symbols represent the mean temperature (°C) for each instar at field conditions, *24.3 ± 1.0; **27.3 ± 2.7; ***28.1 ± 2.4; ****29.8 ± 3.0; *****27.6 ± 3.4

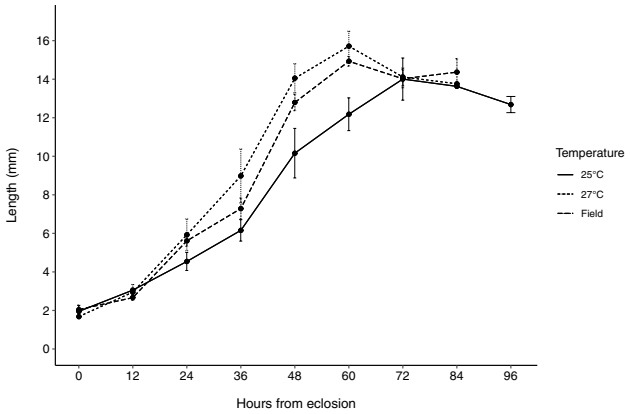

Fig. 2 Mean length of larval instars of *C. megacephala* reared at two constant temperatures (25 °C and 27 °C) and field condition temperatures (27.5 ± 3.2 °C). The dark line connects the mean length data

coordinates of the sampling place [38, 39, 48–59]. Our meta-analysis also included the results of the present study.

The AIC analysis indicated that the developmental time of *C. megacephala* was better explained by the temperature and the latitude and longitude (Table 5; Fig. 3). The duration of the life cycle was negatively influenced by the temperature ($Z = -45.55$, $p < 0.001$). The geographic location (given by the interaction between latitude and longitude) was statistically significant ($Z = -2.40$, $p = 0.0161$). Interestingly, the positive significant interaction between the latitude and the developmental time ($Z = 3.30$, $p < 0.001$) showed that the higher the latitude, the higher the duration of the life cycle ($Z = 2.67$, $p < 0.01$). The same was observed for the longitude. Since not all studies detailed RH information, a linear regression analysis was made between RH and developmental time with the 12 papers that indicated this information. According to this, the RH did not affect the developmental time of *C. megacephala* ($R^2 = 0.04$, $p = 0.22$).

Table 5 Minimum adequate model from the GLM analysis explaining *C. megacephala* development in populations from different locations

Predictor	*Z* value	*p* value
Intercept	151.6	< 0.001*
Temperature	− 45.55	< 0.001*
Lat	3.30	< 0.001*
Long	2.67	< 0.01*
Lat*Long	− 2.40	0.0161*

*Significant difference at a significance level $\alpha = 0.05$

Discussion

The objective of our study was to determine the developmental time of *C. megacephala* under laboratory constant and field temperature conditions. As expected, we found that the life cycle of *C. megacephala* is longer at lower temperatures. We also found no differences in the developmental time of *C. megacephala* between similar temperatures under controlled and field conditions. Moreover, we evaluated the effects of population variations on developmental rates. Our results suggested that the duration of the life cycle of *C. megacephala* depends not only on the temperature but also on the geographic location of the population studied. Data from this study were used to construct the first developmental curve of *C. megacephala* in Mexico.

Insect development is directly related to environmental temperatures due to the characteristic ectothermy of these species [16]. We observed that only 2 degrees of difference are enough to modify the developmental time of the *C. megacephala* of the same population. Many studies on the same species have reported similar results. For instance, Ismail et al. [60] suggested that raising the temperature by 3 °C from 27 °C to 30 °C reduced the total developmental

Table 4 Mean, minimum, and maximum body length of each instar of *C. megacephala* reared at two constant temperatures (25 °C and 27 °C) and under field condition temperatures (27.5 ± 3.2 °C)

Temp °C	Condition	Length (mm)					
		First instar		Second instar		Third instar	
		Mean (± SD)		Mean (± SD)		Mean (± SD)	
		Min (± SD)	Max (± SD)	Min (± SD)	Max (± SD)	Min (± SD)	Max (± SD)
25	Lab	1.9 ± 0.3		3.8 ± 0.7		11.5 ± 2.8	
		1.7 ± 0.3	2.1 ± 0.4	2.7 ± 0.2	4.7 ± 0.3	5.8 ± 0.7	14.6 ± 0.4
27	Lab	1.7 ± 0.2		4.4 ± 1.7		13.3 ± 2.5	
		1.4 ± 0.1	1.9 ± 0.1	2.6 ± 0.3	6.9 ± 0.4	7.0 ± 1.4	16.5 ± 0.6
27.5 ± 3.2	Field	2.0 ± 0.2		4.1 ± 1.6		12.7 ± 2.9	
		1.7 ± 0.1	2.2 ± 0.2	2.6 ± 0.1	7.3 ± 0.5	8.0 ± 0.5	15.1 ± 0.7

No statistically significant differences were found between the mean length of each instar

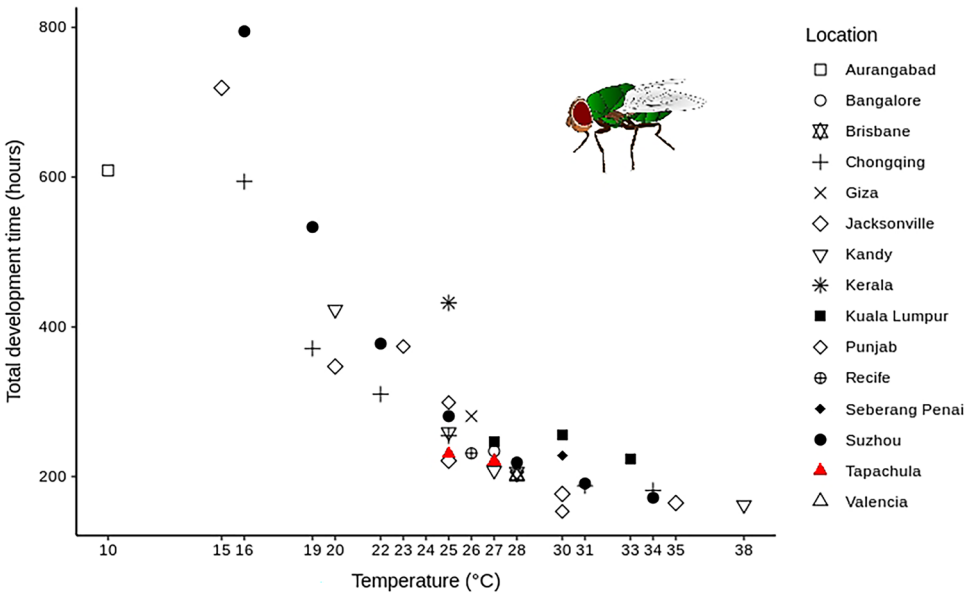

Fig. 3 Developmental time of *C. megacephala* populations from different locations at diverse temperatures. Symbols represent the 15 different studies included in the meta-analysis

time of *C. megacephala* from 8.5 to 5 days. Similarly, Barthi et al. [52] found that the total developmental time of *C. megacephala* was 8.5 days at 28 °C and 5 days at 30 °C. Our meta-analysis results coincide with previous observations that suggest that the duration of the life cycle of *C. megacephala* is negatively influenced by the temperature [24, 39]. Certainly, our results demonstrate that temperature plays a major role in influencing *C. megacephala* developmental rate, ratifying the importance of obtaining the most accurate temperature information at the death scene to estimate a more precise PMI.

Frequently, forensic entomology uses developmental time data generated from controlled assays. However, since ambient temperatures in nature fluctuate over 24-h days, the growth data obtained in these controlled assays do not necessarily reflect the natural developmental rate. In Germany, by using a climatic chamber with temperatures ranging between 5 and 29 °C, Niederegger et al. [61] studied the effect of fluctuating temperatures on the development of different forensically relevant flies and found faster development for *Sarcophaga argyrostoma* and *Lucilia illustris* but slower development for *Calliphora vicina* and *C. vomitoria*. In contrast, our results showed no significant differences between the total life cycle duration at a controlled temperature of 27 °C and that at the field condition temperature of ~ 27.5 ± 3.2 °C. The discrepancies between the study by Niederegger et al. [61] and the present study are likely due to the thermal amplitude evaluated by them in contrast to the low variability of our thermal records. Likewise, research conducted in Australia by Dadour et al. [62] on the forensically relevant fly *Calliphora dubia* indicated no significant differences in the developmental rate of larvae of this fly at fluctuating temperatures between 19 and 30 °C, when compared with a mean constant temperature of 24 °C. Nevertheless, the effect of temperature fluctuations on the developmental time of flies could also be influenced by the geographic location of the populations. This could generate local adaptations and genetic differences in response to different environmental conditions.

The estimation of the PMI is directly related to the age of the oldest species collected from the corpse [9, 10]. While maggots are feeding, their length is considered the best estimator of larval age [63–66]. In this study, we constructed length curves for *C. megacephala*, which contribute as an easy-to-use forensic tool to estimate a more precise PMI in practice. Many studies have already investigated the relationship between the larval body length of *C. megacephala* and developmental duration at constant [50, 57, 67] and fluctuating [68] temperatures. For example, in China (31.3N, 120.8E), Zhang et al. [57] studied larval length changes at seven constant temperatures, which allowed these authors to build an isomegalen diagram, whereas, similarly, Bambaradeniya et al. [58] carried out the first *C. megacephala* developmental studies in Sri Lanka (7.2N, 80.6E), at four constant temperatures. However, the results of these studies show some differences with our present results: while our results in Mexico (14.9N, 92.3W) showed that, at 25 °C, the largest size reached by a third instar larva was 14.8 mm, Zhang et al. [57] measured a mean maximum length of 16.3 mm and Bambaradeniya et al. [58] recorded a mean maximum length of 13.5 mm, at the same temperature. This pattern of increasing larval body size with increasing latitudes has been documented in a variety of studies in insects [69, 70]. Blanckenhorn et al. [71] suggested that this is related to developmental, physiological, and behavioral plasticity.

Blowfly development varied between some studies, despite studying the same variables [24, 57, 73]. According to our meta-analysis results, there is a positive significant interaction between the latitude and the developmental time of *C. megacephala* populations. Although several authors have previously studied the growth rate of *C. megacephala*, results differ from one another, including the present research [24]. While in Punjab, India (31.2N, 74.3E), Bharti et al. [52] showed that the duration of the total life cycle of *C. megacephala* at a constant temperature of 25 °C is 299 h, in Chongqing, China (29.5N, 106.5E), Yang et al. [39] concluded that this species requires 254 h at the same temperature. In line with this, our results about the developmental time of *C. megacephala* in Tapachula, Mexico (14.9N, 92.3W), indicate that colonies develop faster than the populations of the aforementioned localities (231 total h). Similarly, Richards et al. [74] compared the development of various *Chrysomya albiceps* populations and found that developmental zero (D_0; temperature below which development ceases) is directly proportional to the geographic latitude. Trudgill and Perry [75] and Trudgill [76] explained this relationship by proposing that cold-adapted species of high geographic latitude would possess a lower D_0 and would take a longer time to develop than a warm-adapted species of lower geographic latitude and higher D_0. In line with this, Gallagher et al. [73] studied the developmental times of three *L. sericata* populations of the USA and found that populations from cooler climate developed slower than those from warmer climate at the same temperature and suggested the existence of regional variation. They mentioned, for example, that, at 26 °C, populations from San Diego (32.71N, − 117.12W) presented a developmental time 74% slower than those from Massachusetts (42.04N, − 71.07W). Since PMI predictions are associated with blowfly development, understanding its variation should aid our ability to improve PMI predictions.

This variability across latitudes could be a result of phenotypic plasticity or a consequence of genetic adaptation to different thermal environments [77]. Although the mechanisms underlying these phenomena are still unknown, some studies in insects have suggested a positive covariation between genotypes and environments across a latitudinal gradient [79–81]. For example, Hu et al. [82] compared the developmental time of six populations of *C. megacephala* collected from different geographic localities in China, and, to eliminate nongenetic parental thermal environment effects, before the experimental assays, they allowed the population to pass through two generations of identical rearing conditions. Their results indicated genetic differences among populations and variations among populations in thermal reaction norms for developmental time. Similarly, Tarone [72] assessed the genetic effects on blowfly age by evaluating gene expression among three regional strains of *L. sericata.* The author showed that gene expression varies depending on temperature and strain effects, supporting the idea that differences among recorded developmental times could be explained by genetic differences among populations. These backgrounds could be related to the significance of the variables regarding geographic location (latitude, longitude, and their interaction) studied in the present research, and suggest that genetic differences may be the consequence of geographic distance. In line with this, Salem et al. [83] investigated the genetic diversity of *C. megacephala* and found a high intraspecific divergence between populations of four localities from Egypt. In agreement, Chong et al. [84] also observed intraspecific divergence within *C. megacephala* between two Malaysian populations and concluded that the presence of the Titiwangsa mountain range between both localities acts as a natural barrier between the East and West Coast of Peninsular Malaysia. However, before we can fully understand how adaptive plasticity in development and body size can evolve and be maintained, the underlying genetic mechanisms require further study.

Environmental conditions near the equator, with warmer and less fluctuating temperatures, are different from those at higher latitudes. Thus, phenotypic plasticity and genetic adaptation between ectothermic animals may be associated with gradual changes in seasonality and temperatures across latitudes [85]. There are many reports on the developmental time and life history traits of geographically different insect populations. For example, in Australia, located in the southern hemisphere and where the climate ranges from temperate in the south to subtropical in the north, populations of the common brown butterfly, *Heteronympha merope*, from low latitudes have a faster development rate than those from higher latitudes [85]. Similarly, the developmental time of the bee *Exoneura robusta* in Australia has been found to be directly related to the latitude, with more rapid development in northern populations [86], whereas the larval developmental time of the beetle *Colaphellus bowringi* has also been found to be directly associated with increasing latitudes [87]. Regarding Diptera, Khan et al. [88] studied different populations of *Musca domestica* and showed that populations from localities of lower latitudes completed their development faster than those from localities of higher latitudes. However, whether gradual changes in seasonality along the latitudinal gradient were the driving factor of the cogradient variation here observed in *C. megacephala* remains to be corroborated. Since temperature and seasonality co-vary with latitude, it is difficult to isolate their respective impact on adaptive physiological traits. Furthermore, because the studies evaluated through our meta-analysis reared larvae under constant temperatures and photoperiod, quantifying the relative impacts of season length and temperature on physiology is beyond the scope of this study. Further

research on the life history of *C. megacephala* should compare the effects of fluctuating temperatures and photoperiod.

Relative humidity is known to affect diverse physiological parameters in insects [89]. In low RH environments, water loss through the egg and pupal membranes can be detrimental to the survivorship of holometabolous insects, resulting in desiccation [90]. In this regard, Fatchurochim et al. [91] evaluated six forensically important dipteran species (*M. domestica*, *Muscina stabulans*, *Ophyra aenescens*, *Fannia femoralis*, *F. canicularis*, and *Hemetia illucens*) and concluded that their development was successful only when the RH ranged between 40 and 70%. This is in accordance with the studies by Nielsen and Nielsen [92], who demonstrated that, in *C. vicina*, diapause can occur during larval development if the RH is below 40%. In contrast, our findings suggest no effect of RH on *C. megacephala* development. This might be due to the fact that most of the studies using meta-analysis set optimal RH raising conditions. Another explanation could be that the effect of RH is a species-specific relation. In this regard, Fatchurochim et al. [91] found that, within the 40–70% optimal range of RH, the level of humidity did not affect the developmental time of *M. domestica*, *F. femoralis*, *F. canicularis*, or *O. aenescens* but that, in *M. stabulans* and *H. illucens*, developmental time was longer when they were reared at 50% RH than at other humidity levels. Therefore, further studies should be conducted to investigate the duration of the life cycle of Calliphoridae species at constant temperatures but varying RH.

In conclusion, this study provides data on the developmental time of *C. megacephala* and contributes with length curves and ADH tables that can be used to estimate the insect age and can be applied for PMI estimation in criminal investigations. Considering that temperature exposure conditions could affect insect development, we suggest estimating the insect age by using the accumulated degree days/ADH methods, especially when hourly data are obtained, because the accumulated heat required to complete development remains unchanged [78]. Additionally, this is the first work that generates information regarding the development rate of *C. megacephala* populations from Mexico. This contribution is very important considering that the developmental time of *C. megacephala* is affected not only by the temperature but also by the geographic location of the population studied. Currently, estimates of maggot age often depend on reference developmental data from nonlocal populations. However, according to our findings, it is vital to emphasize the importance of advancing the knowledge of the biology of the development of local populations for PMI estimates [5]. This increases the range of possibilities to determine an accurate and reliable PMI in a greater number of forensic cases. Otherwise, if this information is not available, the most appropriate would be to use the developmental time of populations located at similar latitudes and minimal distances.

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Declarations

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Conflict of interest The authors declare no competing interests.

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