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## Life cycle of *Lucilia sericata* (Meigen 1826) collected from Andean mountains

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### ABSTRACT

In forensic science, fly larval size and developmental time help to estimate the time elapsed since a person has died until the body is found, generally known as minimum postmortem interval (mPMI). *Lucilia sericata* (Meigen 1826) is a cosmopolitan and necrophagous fly species (Diptera: Calliphoridae) that usually colonizes decomposing stages. In this study, we determined life tables parameters of *L. sericata* (e.g. fly survivorship, mortality and life expectancy) and developmental time of different larval stages under controlled temperatures. Cohorts of 12 eggs (12 x 10 repetitions) of *L. sericata* were exposed to 8°C, 10°C, 18°C, 25°C, 30°C, 35°C, and 37 ± 0.5°C. We found that larval development was not complete at 8°C and 10°C (minimum temperature limit), and at 35°C and 37°C (maximum temperature limit). The number of larvae that reached the adult stage was similar ( $F_{2,30} = 0.20$ ,  $p = 0.814$ ) at all viable temperatures (18°C, 25°C, and 30°C). We found the highest mortality to occur at initial developmental stages. Under viable temperatures, the developmental time of *L. sericata* from egg to adult decreases with temperature, with an average of 778 h at 18°C, 401 h at 25°C, and 288 h at 30°C. The developmental time of *L. sericata* at the fastest temperature (778 h) is similar to that found in Vienna (Austria), but it is 2–3 times slower than that in three cities across the United States. These results will improve the estimation of mPMIs in tropical countries across the Andes region

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Andes; developmental stages; life table; post mortem interval (PMI); temperature; tropical countries

## Introduction


Medico-legal Entomology (M-LE) studies the insects associated with decomposing corpses [1] and provides useful data for suicide, homicide, and unexplained death cases [1,2]. The time taken by necrophagous insects to reach their different developmental stages allow forensic scientists to estimate the minimum postmortem interval calculation (mPMI), defined as the time after death, from when the corpse was exposed to insects, until the body is discovered [2,3]. There are two ways to calculate the a mPMI. The first one uses the age of the larvae and their developmental rate [4]. Larval infestations help to estimate the mPMI by calculating the age of the oldest cohort of larvae found in the corpse [5]. The second one looks at successional stages of insect communities at the decomposing body, and it is mostly useful to calculate mPMI at the latest stages of decomposition [4].

While developmental rates of necrophagous species vary with relative humidity and diet, the most significant factor affecting developmental time is temperature [6], therefore a large proportion of M-LE research determine the life cycle of necrophagous species under different temperatures, mimicking local variability [7]. When studying the life cycle of a fly species, it is necessary to determine survivorship

rates; to accomplish this, life tables are recorded from fly cohorts monitored at lab conditions [8]. Previous studies showed that at higher temperatures life cycles get shortened. This may be because dipterans are poikilothermic in nature, and thus biochemical processes are positively correlated with temperature [9]. However, few studies come from tropical regions, where the temperature is relatively constant through the year.

*Lucilia sericata* is a necrophagous and cosmopolitan fly distributed widely in Ecuador, including Pichincha Province and Quito, the capital of the country [10,11]. *L. sericata* is one of the species that first arrive to carrion and could be essential to calculate the mPMI [6,12]. In medicine, *L. sericata* is known to cause cutaneous myiasis [12,13]. However, larvae of *L. sericata* have antibacterial substances that help to scar [14]. So, it is also used in maggot debridement therapy where laboratory sterile larvae feed on necrotized tissue of patients' wounds [14]. Finally, *L. sericata* is a synanthropic species; and knowing the biological cycle of *L. sericata* can enhance forensic research in urban and rural areas [6].

Populations of *L. sericata* can adapt to local environmental conditions, such as topography, humidity, photoperiod, vegetation, and food [5]. One of the most important factors that impacts the life cycle of

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*L. sericata* is temperature. Grassberger and Reiter [15] studied the life cycle of a population of *L. sericata* in Vienna (Austria) at temperatures ranging between 15°C and 34°C; and studied the effects that different temperature regimes had on larvae length. On the other side of the Atlantic Ocean, Gallagher et al. [5] conducted essays at 16°C, 26°C, and 36°C to determine the variation of the developmental time in three geographically distant fly populations (i.e. Sacramento, San Diego, and Easton) of the United States. The time to complete a life cycle varied between populations, with longer developmental time found between 16°C and 26°C in Easton, and at 36°C in San Diego. This variability in fly development across geography suggests that measuring the impacts of temperature on life cycles, for different fly species, should be a task of M-LE research.

In this study, we recorded the life tables of *L. sericata* at controlled lab conditions; in particular, we studied the influence of temperature over developmental time and survivorship of *L. sericata*'s individuals. In addition, we determined the minimum and maximum temperature limits of development, defined here as the temperatures that halt (or slow-down) fly development [16–18]. These variables will help forensic scientists to estimate the time that has elapsed since a person has died, as the minimum temperature for fly development is part of the mPMI equation [19].

## Materials and methods

### Locality

Flies used in this study comes from Quito, at 2850 m of elevation, with daily temperatures that fluctuate between 10 a 27°C, and an average annual temperature of 13.9°C [20]. Adults were identified with taxonomic keys [21]. The greenhouse is located in the urban area of the city, at the QCAZ (Quito-Católica-Zoología) museum at the Pontificia Universidad Católica del Ecuador, and has an average environmental temperature of 17°C. *L. sericata* was reproduced in plexiglass boxes of 40 cm × 40 cm. Egg collection was achieved by placing meat at sunset, when adult activity is null, and then collecting the meat by 8:00 am. By placing the meat after sunset, we ensure that eggs were recently oviposited. The eggs were then separated from the meat using a brush and assigned to a treatment.

### Experimental design

Seven thermal treatments were established (8°C, 10°C, 18°C, 25°C, 30°C, 35°C, and 37°C ± 0.5°C). We used a total of 12 eggs per replicates, for a total of 10 replicates per treatment. Each replicate was placed

on a plastic container (12 oz capacity) and fed with a piece of meat (20 g of lean beef muscle). Plastic containers were equipped with a fabric mesh placed on top of the lid to allow air circulation. The meat was placed on a piece of aluminum foil to avoid fluid leakage. Excess fluids by meat decomposition were absorbed by a 2.5 cm layer of diatomites placed at them bottom of the container.

All eggs in each replicate came from the same egg batch. A climatized chamber kept constant experimental temperatures and relative humidity of 70% ± 15%. This relative humidity prevents desiccation of the larvae [22,23]. Experiments underwent a photoperiod of 12 h, from 06:00 am to 06:00 pm. The climatized chamber was locally produced, and has an automatic light control timer, a heater and a humidifier controlled by a Full Gauge controller. Temperature and relative humidity were verified using a HOBO U23 Pro v2 Temperature/Relative Humidity Data Logger.

### Life tables

We filled horizontal life tables [24] that measured several vital statistics:  $N_x$  = Number of individuals in  $x$  stage.  $I_x$  = Proportion of survivors in  $x$ , ranges from 1 (all survived) to 0 (all died).  $d_x$  = Number of individuals that die between  $x$  and  $x + 1$ . The probability of dying between  $x$  and  $x + 1$ ,  $q_x$ , ranges from 1 (all died) to 0 (all survived). And,  $e_x$  = life expectancy (in time units expressed in days). To visualize survivorship through time, we built survivorship curves using the number of individuals that survived in each stage [25]. Our life tables were done with all developmental stages, from egg to pupa (adult hatching); life span of adults was not included since it is not necessary to calculate the minimum PMI.

### Larval developmental time

*L. sericata* has a complete metamorphosis (holometabolism) that includes the following stages: egg, three larval stages (first–third instar), pupa, and adult [26]. We measured time in hours of development from egg to larva 1 (L1), L1-L2, L2-L3, L3 to pupa, and from pupa to adult; larvae were observed twice a day, once at 8:00 am and a second time at 4:00 pm until the end of the end of the experiment. To determine larval stage, we used a stereoscope (Leica MZ75) and assessed the following characters located in the posterior spiracles: number of openings in the posterior spiracle, the presence of a well-developed peritreme, and the status of a button (either well-defined or not). In L1, there is one opening in the posterior spiracle, and the peritreme and the button are not defined. L2 is the same as L1 except for the appearance of a second opening in the posterior spiracle. In L3, the

peritreme and the button are now well-defined, and the posterior spiracle has three openings [27,28]. Within experimental temperatures, minimum and maximum temperature limits were defined as temperatures where there was no larvae development [16–18].

### Statistical analyses

ANOVA was used to verify if the temperature has an effect on developmental time and survivorship within the cohorts. Parametric tests of homogeneity of variance (Levene) and normality of response variables (Kolmogorov-Smirnov) were performed. *P*-values were considered significant at 0,05. Post-hoc differences between treatments were assessed with a Tukey's HST.

## Results

### Lifetables

Table 1 shows the life table parameters of *L. sericata* cohorts under different experimental temperatures. At the coldest temperatures, i.e. 8°C and 10°C, there was not fly development, with flies dying at egg and L1 stage. Thus 10°C was deemed *L. sericata* minimum temperature limit. At the other side of the temperature range, at 35°C it was observed that larval development slowed down, most larvae got dehydrated, and only 0,3 individuals (or 2.5% of all experimental flies) made it to the adult stage (Table 1). Moreover, at 37°C, all flies but one were

dead by L3. Thus, 35°C was deemed *L. sericata* maximum temperature limit. The ANOVA and Turkey's tests on survivorship showed two different groups, the first one confirmed by low and high temperatures (i.e. 8°C, 10°C, 35°C and 37°C) treatments, and the second one by viable temperatures, e.g. 18°C, 25°C, and 30°C treatments (Figure 1;  $p < 0,001$ ).

Among viable temperatures, the number of survivors that completed their development to adults was around 7.1 individuals. The highest mortality ( $q_x$ ) among these viable temperatures was found between egg to L1, with a second peak between L3 to pupa.

### Larval development

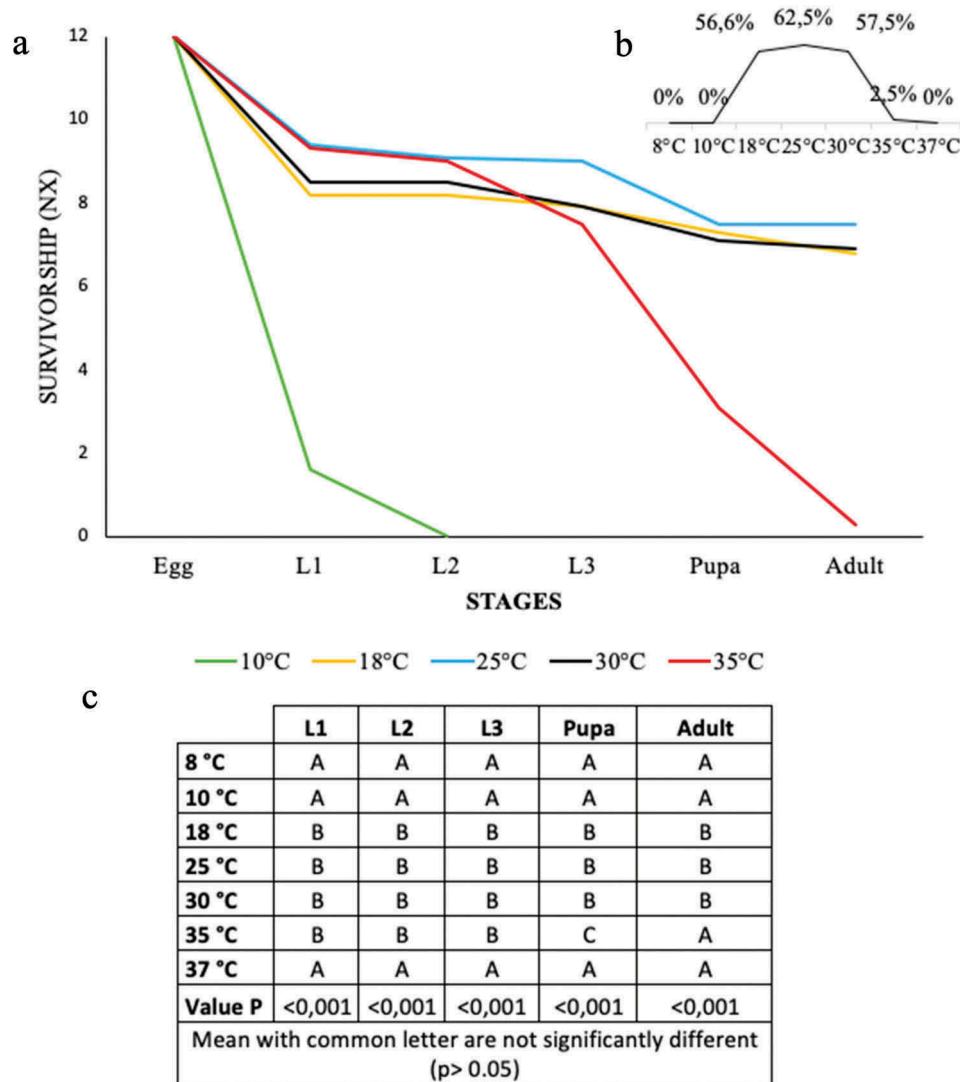
Complete life cycles, from eggs to adults, were observed for viable temperature (Table 2). At 18°C, the average developmental time was 778 h ( $\pm 38,6$ ); at 25°C average time was 401 h ( $\pm 33,5$ ); and at 30°C average time was 288 h ( $\pm 24,8$ ). Under these experimental temperatures, it is noticeable that developmental time shortens at higher temperatures ( $p < 0,001$ ). Tukey's HST showed that each of these temperatures were different among each other (Table 2).

## Discussion

Thermal limits of forensic fly species are of interest. This study provides information about the importance of local temperature in the development of *L. sericata*. We found that for *L. sericata* the minimum

**Table 1.** Life tables of *L. sericata* under experimental temperatures. Only temperatures for viable (where most egg hatched adults) are depicted.  $N_x$ = number of larvae in stage  $x$ ;  $l_x$ = proportion of survivors in stage  $x$ ;  $d_x$ = number of individuals that die between  $x$  and  $x + 1$ ;  $q_x$ = probability to die between  $x$  and  $x + 1$ ;  $e_x$ = life expectancy expressed in days. For example, out of 12 eggs subjected to 18°C ( $N_x$ ) at the beginning of the experiment, 6,8 reached the adult stage, where L1 survived in higher proportion ( $l_x$ ) out of the whole cohort with 0.68; highest number of dead larvae ( $d_x$ ) occurred in the egg stage before transitioning into L1 with a total of 3,8 individuals, therefore the highest probability of death ( $q_x$ ) occurs during the egg stage, followed by L3 before transitioning into the pupal stage with 0,32 and 0,08, respectively; longer life expectancy ( $e_x$ ) occurs during L2 stage with a life expectancy of 3,76 days.

Temp.	Stage	$N_x$	$l_x$	$d_x$	$q_x$	$e_x$
18°C	<b>Egg</b>	12				
	<b>L1</b>	8,20 ( $\pm 1,2$ )	0,68 ( $\pm 0,1$ )	3,80 ( $\pm 1,2$ )	0,32 ( $\pm 0,1$ )	3,42 ( $\pm 0,5$ )
	<b>L2</b>	8,20 ( $\pm 1,2$ )	0,68 ( $\pm 0,1$ )	0,00 ( $\pm 0,0$ )	0,00 ( $\pm 0,0$ )	3,76 ( $\pm 0,2$ )
	<b>L3</b>	7,90 ( $\pm 1,4$ )	0,66 ( $\pm 0,1$ )	0,30 ( $\pm 0,5$ )	0,04 ( $\pm 0,1$ )	2,76 ( $\pm 0,2$ )
	<b>Pupa</b>	7,30 ( $\pm 1,8$ )	0,61 ( $\pm 0,1$ )	0,60 ( $\pm 0,7$ )	0,08 ( $\pm 0,1$ )	1,84 ( $\pm 0,2$ )
	<b>Adult</b>	6,80 ( $\pm 1,7$ )	0,57 ( $\pm 0,1$ )	0,50 ( $\pm 0,5$ )	0,07 ( $\pm 0,1$ )	0,96 ( $\pm 0,0$ )
25°C	<b>Egg</b>	12				
	<b>L1</b>	9,40 ( $\pm 2,5$ )	0,78 ( $\pm 0,2$ )	2,60 ( $\pm 2,5$ )	0,22 ( $\pm 0,2$ )	3,73 ( $\pm 0,9$ )
	<b>L2</b>	9,10 ( $\pm 2,7$ )	0,76 ( $\pm 0,2$ )	0,30 ( $\pm 0,5$ )	0,04 ( $\pm 0,1$ )	3,62 ( $\pm 0,3$ )
	<b>L3</b>	9,00 ( $\pm 2,7$ )	0,75 ( $\pm 0,2$ )	0,10 ( $\pm 0,3$ )	0,01 ( $\pm 0,0$ )	2,73 ( $\pm 0,2$ )
	<b>Pupa</b>	7,50 ( $\pm 2,5$ )	0,63 ( $\pm 0,2$ )	1,50 ( $\pm 1,4$ )	0,16 ( $\pm 0,1$ )	1,76 ( $\pm 0,2$ )
	<b>Adult</b>	7,50 ( $\pm 2,5$ )	0,63 ( $\pm 0,2$ )	0,00 ( $\pm 0,0$ )	0,00 ( $\pm 0,0$ )	1,00 ( $\pm 0,0$ )
30°C	<b>Egg</b>	12				
	<b>L1</b>	8,50 ( $\pm 2,5$ )	0,71 ( $\pm 0,2$ )	3,50 ( $\pm 2,5$ )	0,29 ( $\pm 0,2$ )	3,45 ( $\pm 0,9$ )
	<b>L2</b>	8,50 ( $\pm 2,5$ )	0,71 ( $\pm 0,2$ )	0,00 ( $\pm 0,0$ )	0,00 ( $\pm 0,0$ )	3,67 ( $\pm 0,3$ )
	<b>L3</b>	7,90 ( $\pm 2,4$ )	0,66 ( $\pm 0,2$ )	0,60 ( $\pm 1,0$ )	0,07 ( $\pm 0,1$ )	2,67 ( $\pm 0,3$ )
	<b>Pupa</b>	7,1 ( $\pm 2,6$ )	0,59 ( $\pm 0,2$ )	0,80 ( $\pm 1,1$ )	0,10 ( $\pm 0,2$ )	1,83 ( $\pm 0,2$ )
	<b>Adult</b>	6,90 ( $\pm 2,6$ )	0,58 ( $\pm 0,2$ )	0,20 ( $\pm 0,4$ )	0,03 ( $\pm 0,1$ )	0,98 ( $\pm 0,0$ )



**Figure 1.** a) Survivorship curves of *L. sericata* under experimental temperatures. b) The figure shows the percentage of survivors at experimental temperatures. c) Tukey's HST; significance at 0,05.

**Table 2.** Average number ( $\pm$  standard deviation) of hours of development for the five stages of *L. sericata* life cycle (egg, L1, L2, L3, and pupa) under experimental temperatures. For example, at 18°C, individuals took 778 h before they reached the adult stage. Out of those 778 h, individuals stayed on average in the egg and L1 stage for 36 h; 55 h in L2; 276 h in L3; and 374 h in the pupa stage. Tukey's HST found three groups among viable temperatures.

	8°C Hours	10°C Hours	18°C Hours	25°C Hours	30°C Hours	35°C Hours	37°C Hours
Egg	-	102 ( $\pm 53,1$ )	36 ( $\pm 0,0$ )	24 ( $\pm 0,0$ )	12 ( $\pm 0,0$ )	24 ( $\pm 0,0$ )	12 ( $\pm 0,0$ )
L1	-	-	36 ( $\pm 0,0$ )	12 ( $\pm 0,0$ )	12 ( $\pm 0,0$ )	12 ( $\pm 0,0$ )	12 ( $\pm 0,0$ )
L2	-	-	55 ( $\pm 6,3$ )	36 ( $\pm 0,0$ )	24 ( $\pm 0,0$ )	12 ( $\pm 0,0$ )	24 ( $\pm 0,0$ )
L3	-	-	276 ( $\pm 19,9$ )	122 ( $\pm 21,1$ )	86 ( $\pm 12,4$ )	163 ( $\pm 108,4$ )	-
Pupa	-	-	374 ( $\pm 12,4$ )	206 ( $\pm 12,4$ )	154 ( $\pm 12,4$ )	161 ( $\pm 27,7$ )	-
Total	-	-	<b>778 (<math>\pm 38,6</math>)</b>	<b>401 (<math>\pm 33,5</math>)</b>	<b>288 (<math>\pm 24,8</math>)</b>	<b>372 (<math>\pm 136,1</math>)</b>	-
Tukey's HST	-	-	<b>a</b>	<b>b</b>	<b>c</b>	-	-

temperature limit was 10°C; at this temperature, there was no development. These limits are similar to other studies have reported a minimum temperature of 10°C [17,29]. Similarly, Gennard [19] in his book *Forensic Entomology* reported that the lower thermal limit of *L. sericata* is 9°C. On the other side, the maximum temperature limit was 35°C, at this temperature larval development was also slowed down. Survivorship of adults was very low (2.5%), the majority of individuals

died dehydrated at the L3 stage. These results are similar with the study conducted in the USA by Gallagher et al. [5], where they found that the upper thermal limit was slightly higher (36°C) than in our experiment.

Intermediate temperatures, e.g. 18°C, 25°C, and 30°C, were found optimum for development from egg to adult stage. Among these viable temperatures, we found that at higher temperatures the

**Table 3.** Total hours of development of *L. sericata* life cycle reported in this study in comparison with the results reported by Grassberger and Reiter [15], and Gallagher et al. [5]. ND stands for No Development.

	This study	Grassberger and Reiter [15]	Gallagher et al. [5]		
			Sacramento	San Diego	Easton
R.H	70%	60%		65–75%	
Photop.	12 h	12 h		16 h	
8°C	ND				
10°C	ND				
15°C		ND			
16°C			208	185	211
17°C		842			
18°C	778				
19°C		564			
20°C		451			
21°C		379			
22°C		339			
25°C	401	297			
26°C			76	76	103
28°C		275			
30°C	288	268			
34°C		259			
35°C	372				
36°C			65	74	67
37°C	ND				

developmental time shortens, a pattern similar to that of Grassberger and Reiter [15], and Gallagher et al. [5]. However, there are differences in developmental times between these three studies (Table 3), which could be explained as a population-level adaptation to the different environmental conditions that occur in different geographic regions [16,30]. The developmental time of *L. sericata* at the fastest temperature (778 h) is similar to that found in Vienna (Austria), but it is 2–3 times slower than that in three cities across the United States, suggesting strong differences in the development of flies between Europe and the United States.

Life tables found that there were no differences in the number of flies that reach the adult stage across viable temperatures. Most mortality in these treatments occurred between the egg and L1 stages, meaning that the eggs did not hatch. While there may be several reasons behind egg mortality (high egg mortality may occur from both unmated females, and protein-deprived females [31]) the reasons for high egg mortality in our experiment remain unexplained. A great number of individuals died in L3 stage, before the pupal stage. This could have happened due to the molting enzymes becoming inactive. These enzymes are highly sensitive to temperature and pH, and if the temperature they are subjected to is not ideal, enzymes could decrease their activity or become inactive [32]. Hormonal processes are required for the transition from one stage to the next one to take place, and if high or low temperatures affect the normal performance of the juvenile hormone, it is possible that pupation may not happen. Molting processes are regulated by this

hormone, which in high concentrations during the larval stage inhibits the expression of adult characteristics, therefore, if the levels of this hormone remain high in the post-feeding stage, the larva may not pupate and it will die [33].

Knowing the biology of species of forensic interest under laboratory conditions has become a great tool for forensic researchers, as this information is highly relevant to determine the minimum postmortem interval calculation. With the information generated in this study, it is possible to estimate the minimum PMI through the calculation of the Accumulated Degree Hours (ADH) or the Accumulated Degree Days (ADD) [16,17,19]. To perform this calculation it is necessary to have the information about the developmental time needed to reach a specific stage under constant temperature [16,17,19]. It is also important to know the minimum temperature for development or base temperature, i.e. 10°C for *L. sericata* [29, and this study]. The equation is as follows: Time expressed in hours  $\times$  (temperature – base temperature) = ADH, Time expressed in days  $\times$  (temperature – base temperature) = ADD [17,19].

Below we present an example of the estimation of the minimum PMI in a hypothetical case (for the calculation we use Gennard [19] equation):

On November 17, at 1:00 pm, a lifeless body was found in the area of Guápulo. When collecting entomological evidence from the body, first instar larvae of the blow fly species *Lucilia sericata* were found. In the laboratory, it was determined that at a constant temperature of 18°C the larvae need 36 h to develop from egg to larva. Meteorological records of the area showed that the average temperature on November 17 was 14.3°C and was 15°C on the 16th.

Required temperature for the fly to transition from egg to 1st instar larvae:

$$\text{Time}_{(\text{hours})} \times (\text{Temperature} - \text{base temperature})$$

ADH calculation under controlled temperature

$$36 \text{ hours} \times (18 - 10^\circ\text{C}) = 288 \text{ ADH}$$

$$\text{Nov 17, insects accumulated ADH} = 13 \text{ h} \times (14.3^\circ\text{C} - 10^\circ\text{C}) = 55.9 \text{ ADH}$$

$$\text{Nov 16, insects accumulated ADH} = 24 \text{ h} \times (15^\circ\text{C} - 10^\circ\text{C}) = 120 \text{ ADH}$$

Values of ADH of both days are added to know the caloric energy obtained in the two days (55.9 + 120 = 175.9 ADH).

This value is subtracted from the total value needed for the larva to reach the 1st instar (288 ADH – 175.9 ADH = 112.1 ADH)

$$\text{The obtained value } 112.1 \text{ ADH} \div (14.7^\circ\text{C} - 10^\circ\text{C}) = 23.8 \text{ h}$$

Thus, it can be concluded that this person died at or earlier than on November 15 around 1:00 am.

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