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ORIGINAL ARTICLE

Estimating the age of immature *Chrysomya albiceps* (Diptera: Calliphoridae), correcting for temperature and geographical latitude

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Abstract Developmental curves for *Chrysomya albiceps* (Wiedemann) (Diptera: Calliphoridae) were established at 13 different constant temperatures using developmental landmarks and length as measures of age. The thermal summation constants (K) and developmental zeros (D_0) were calculated for five developmental landmarks using the method described by Ikemoto and Takai (Environ Entomol 29:671–682, 2000). Comparison with the K and D_0 values of our findings to those of three previously published studies of *C. albiceps* suggests that K is directly proportional to geographic latitude, and D_0 is inversely proportional to both K and geographic latitude. Body size and developmental landmarks have a complex relationship because of trade-offs between mortality risk and female fecundity (as measured by body size) at non-optimal temperatures. This relationship can be summarized using superimposed isomorphen and isomegalen diagrams, which can then be used to make forensic estimates of postmortem intervals from larval body lengths. Finally, we recommend that future studies providing data for precise forensic estimates of postmortem intervals should use a relative temporal precision of about 10% of the total duration being measured. For many blowflies, this translates into a sampling interval of approximately every 2 h before hatching, 3 h before first ecdysis and 6 h before second ecdysis.

Keywords Forensic entomology · *Chrysomya albiceps* · Calliphoridae · Development rate · Developmental zero (D_0) · Thermal constant (K) · Geographic latitude · Postmortem interval

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Introduction

A major use of forensically important insects is to estimate the time between death and the discovery of a corpse, known as the postmortem interval (PMI). Because blowflies are often the first insects to arrive on a corpse, the focus of these estimates is on them.

Chrysomya albiceps (W.) is widely distributed throughout Africa, South America, and parts of Europe and Asia [14, 24, 30, 41, 45]. It causes myiasis in humans and livestock, feeds on carrion and human feces, and breeds prolifically in carrion [14, 45], making it a medically, veterinarily, sanitationarily, and forensically important fly. It is also ecologically significant, being a predator of other dipteran larvae, and its maggots are frequently found around the periphery of corpses [3, 40].

The most common method used to calculate PMI is the thermal summation or accumulated degree day/hour model, a linear regression model based on the temperature-dependent rate of development of immature insects [4, 15]. The duration of development of immature stages is measured at any number of constant temperatures, which are plotted on a graph relating duration of development (x-axis) and the product of the duration of development and time (y-axis) [21]. The precision of the estimate is affected by the number of constant temperatures used in the regression analysis, and good regression models are based on no fewer than six points along the linear section of the regression [21]. The y-intercept (thermal summation constant, K) and slope (developmental zero, D_0) from the resultant regression line are used to calculate PMI [4, 16, 15].

Despite the importance of an understanding of the rate of development in relation to temperature, few authors have published on this topic using *C. albiceps* (Table 1). Queiroz [33] timed development at four different constant temper-

Table 1 Development zero and thermal summation constants for five developmental events for *C. albiceps* calculated using the analytical method described by Ikemoto and Takai [21]

	Developmental zero		Thermal summation constant		r^2	*N* used for analysis	*N* rejected from analysis
	°C	Standard error	h°C	Standard error			
Hatching							
Grassberger et al. [14]	9.72	0.67	258.30	17.39	0.97	5	0
1st ecdysis							
This study	11.14	0.27	655.63	23.03	0.99	7	5
2nd ecdysis							
This study	13.00	0.74	984.71	84.40	0.98	7	4
Onset of wandering							
Queiroz [33]	15.01	0.54	1593.72	160.75	1.00	4	0
This study	13.92	0.99	2238.98	210.56	0.98	7	4
Onset of pupariation							
Queiroz [33]	14.63	0.64	1997.09	212.58	1.00	4	0
This study	13.65	0.68	2354.34	207.55	0.99	7	4
Grassberger et al. [14]	11.65	0.08	2819.00	15.48	1.00	4	0
Marchenko [26]	10.21	–	2948.11	–	–	18	0
Eclosion							
Queiroz [33]	16.52	0.49	2845.89	286.54	1.00	3	0
This study	13.64	1.14	4138.79	429.27	0.97	7	1
Grassberger et al. [14]	10.10	0.53	7861.04	169.29	0.99	4	0
Marchenko [26]	10.21	–	4442.40	–	–	18	0

Studies are placed in order of absolute latitude within events.

atures, Grassberger et al. [14] timed it at five constant temperatures, and Marchenko [26, 27] presented calculations for 18 different temperatures from an unpublished data set. Ullyett [40] and Prins [31] published anecdotal data at single temperatures. No author recorded developmental rates for more than three developmental events, and the results of the studies are apparently not in agreement.

In this paper, we present development rates for *C. albiceps* at 13 different constant temperatures for five developmental events and calculate the associated thermal summation constant (measure of thermal time taken to reach each developmental event, K) and developmental zero (temperature below which development ceases, D_0) values. In addition to this, we compare the K and D_0 of our findings to those of published data to explore the disparities between the studies.

Materials and methods

About 70 adults of *C. albiceps* were collected with a Red Top® fly trap (Miller Methods, Pretoria, South Africa) in Grahamstown (33°19′S:26°32′E), South Africa, to start a laboratory culture. The culture was maintained within 2° of 22°C under a lighting cycle of 12:12 h (light/dark). Flies were fed with milk powder, sugar, and water ad libitum for 1 week and then provided with a 200-g pork chop as an oviposition medium. Numerous eggs were found on the underside of the chop after 1 day and were monitored frequently until they hatched. The duration between oviposition and hatching was not recorded because of uncertainty about the timing of oviposition and about the occurrence of precocious egg development in the maternal oviducts [43].

Newly hatched larvae (approximately 1 h old) were placed ten to a cup in tapered, plastic 250 ml cups, each containing 20 g of fresh chicken liver. This low density of maggots prevented measurable temperature increases from maggot-generated heat [11] that might have stimulated growth [16] and avoided stunted growth associated with isolation [9]. Each cup was steadied in 3.0–3.5 cm of river sand within an empty 8×8×5 cm plastic tub. This provided sufficient sand for pupariation once larvae began to wander. Cups were placed in Labcon 3104 U incubators, each incubator set at a different constant temperature, ranging from 15 to 45°C at 2.5°C intervals. To avoid stunted growth and cannibalism, additional chicken liver was added when the original food dried out or was consumed.

Twice a day, five random maggots were sampled, each from a different cup, at each temperature and placed directly into 70% alcohol. The rapid development of blowflies at high temperatures and the high number of cups used at low temperatures allowed some larvae from all cups to reach pupariation. Larvae took between 1 and 2 h to die, after which each maggot's instar was recorded and its length was measured to 0.1 mm using a gauge described by

Villet [42]. This relatively short period in alcohol minimized the effect of shrinkage or expansion of maggots due to preservation but was sufficient to kill them. Samples were placed directly into alcohol and not killed in hot water because this is standard procedure in South Africa when collecting entomological evidence from a crime scene.

Length vs developmental event as a measurement of age

Isomorphen and isomegalen diagrams [12] were constructed using the computer programs "Microsoft Excel 2003" and "Statistica 7" and then overlaid (Fig. 1) to compare length and developmental events as estimates of age.

Thermal summation constant (K) and development zero (D_0)

By plotting the cumulative proportion of each phase of development represented in each sample, the median durations of all phases were calculated to a precision of hours. Reduced major axis regression was used to calculate K and D_0 from the median durations [21] using the computer program "Statistica 7". In addition, K and D_0 values were calculated in the same way for three published studies [14, 26, 27, 33].

Results

Development rates for both larval and puparial stages increased steadily with increasing temperatures (Fig. 1). Larvae reached second instar as late as 8.5 days after hatching at 15°C and as early as half a day at 40 and 42°C. The longest minimum larval development period (duration to the onset of pupariation) and minimum pre-imaginal development periods (duration from hatching to the onset of eclosion) were 22.5 and 28 days at 17.5 and 20°C, respectively, and the shortest were 5.5 and 9 days at 30 and 35°C, respectively (Fig. 1).

The largest maggot measured was 16.2 mm long at 25°C. Larvae reached larger average sizes at higher temperatures (Fig. 1) and pupariated at significantly shorter lengths below 20°C (F=79.47; p=0.00). No larvae survived to pupariation at 15 or 45°C, no pupae eclosed at 17.5, 40, or 42.5°C, and eclosion rates were poor above 35°C (Fig. 1). The highest pupariation survival rate was at 20 and 22.5°C, although both the greatest numbers of puparia (49) and adults (48) were both recorded at 32.5°C.

Length vs developmental event as a measurement of age

The contour of each developmental event in the isomorphen diagram frequently intersects numerous body length contours of the isomegalen diagram, several of which cross more than one developmental contour (Fig. 1).

Thermal summation constant (K) and development zero (D_0)

Development data from extreme temperatures are not used in thermal summation models based on linear regression

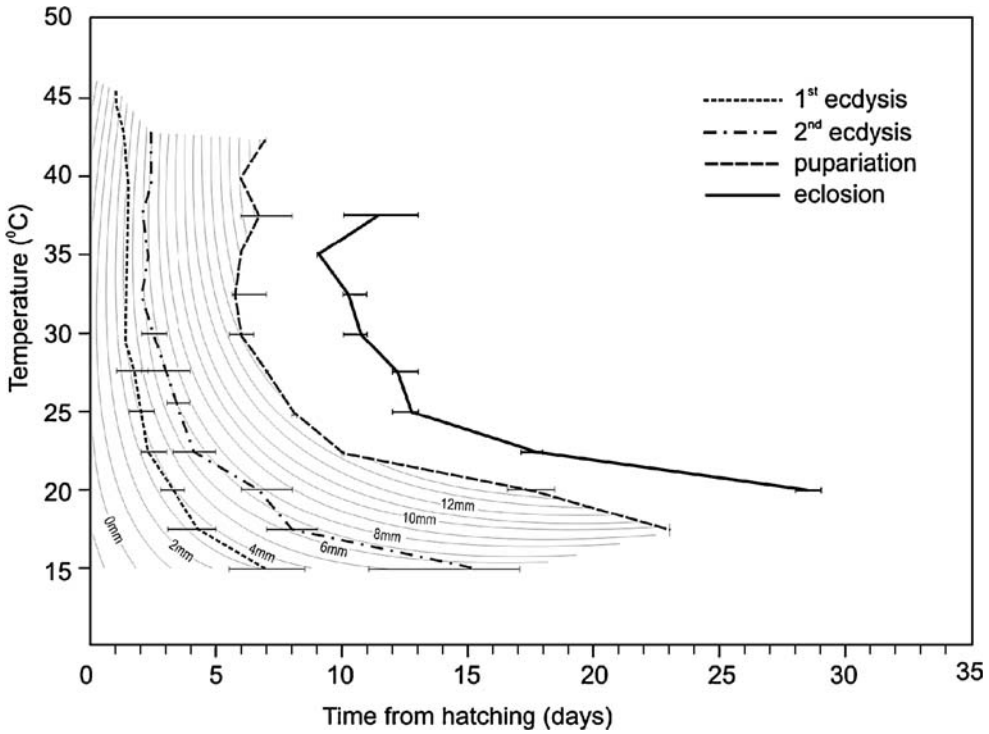


Fig. 1 Superimposed isomorphen and isomegalen diagrams. The contours of the isomegalen diagram are interpolated using the "distance

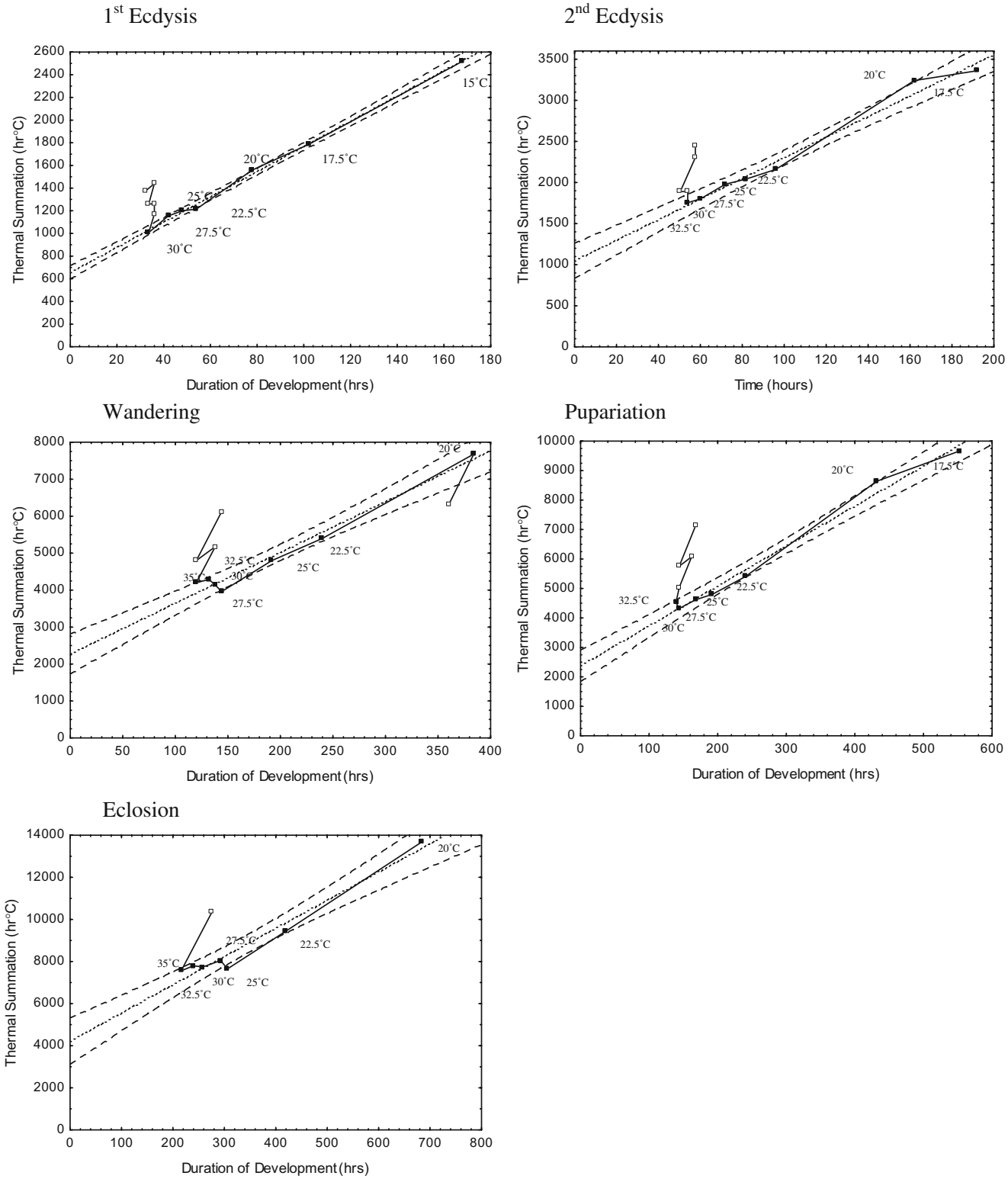


Fig. 2 S-shaped curves and reduced major axis regression lines used to determine K and D_0 values of *C. albiceps* at 13 different temperatures for the first ecdysis, second ecdysis, onset of wandering, onset of pupariation, and eclosion. *Black squares* indicate points used in the regression calculations, *white squares* indicate points not used in the calculations because they are not on the linear part of the relationship [21], and *dotted lines* represent 95% confidence intervals

because these points do not lie on the straight section of the developmental curve and should therefore be excluded from the regression analysis [16, 21]. Using criteria described by Ikemoto and Takai [21], we limited our analyses to colinear data points for each developmental event (Fig. 2), and calculated D_0 and K for five developmental events. The fit of the models was excellent, with high coefficients of determination (Table 1) and narrow confidence intervals (Fig. 2). D_0 and K were, respectively, 11.14°C and 655.63 h°C for first ecdysis, 13.00°C and 984.71 h°C for second ecdysis, 13.92°C and 2,238.98 h°C for onset of wandering, 13.65°C and 2,354.34 h°C for onset of pupariation, and 13.64°C and 4,138.74 h°C for eclosion. The average D_0 for all developmental events was 12.99°C (n=5 events; standard error=0.51°C).

The same analysis was applied to published studies of development in *C. albiceps* using as many points from each study as meeting the selection criteria [21]. All models showed high r^2 values (Table 1) and narrow confidence intervals (Fig. 3) except for that of eclosion in the Brazilian fly population. For flies from Moscow [26, 27], the average D_0 was 10.21°C (n=2 events; standard error=0.00°C); from Vienna [14], 10.49°C (n=3 events; standard error=0.59°C); and from Rio de Janiero [33], 15.39°C (n=3 events; standard error=0.58°C). None of the 95% confidence intervals overlapped, except between Moscow and Vienna, and the values are in the same rank order as the absolute latitudes of the locations (Fig. 4a). Values for K were generally inversely proportional to D_0 (Fig. 4b) and therefore proportional to absolute latitude (Fig. 4a).

Discussion

Developmental optima

Larvae of the Grahamstown population developed poorly outside a temperature range of 20–40°C. While growth rates were maximal at the highest temperature (Fig. 1), survivorship and condition were better at lower temperatures. Similarly, pupae developed best between 20.0 and 32.5°C, which is an even narrower temperature window. The sigmoidal shape of plots of temperature against developmental rate indicates that there is an optimum temperature for development, which would lie at the inflection of the sigmoid. Moving away from this optimum, growth becomes increasingly compromised, so that while larvae grow faster at higher temperatures, they incur increasing levels of physiological stress that are expressed as slightly smaller mature sizes and distinctly lower survivorship. Similarly, at lower temperatures, development is increasingly retarded to the point where larvae will pupate at uncharacteristically small sizes rather than spend more time attempting to reach their usual mature size (Fig. 1). The decrease in survivorship at lower temperatures is more precipitous than it is at higher temperatures (Fig. 2), indicating that the physiological stresses that impede growth are different on either side of the optimum.

Length vs landmarks as a measurement of age

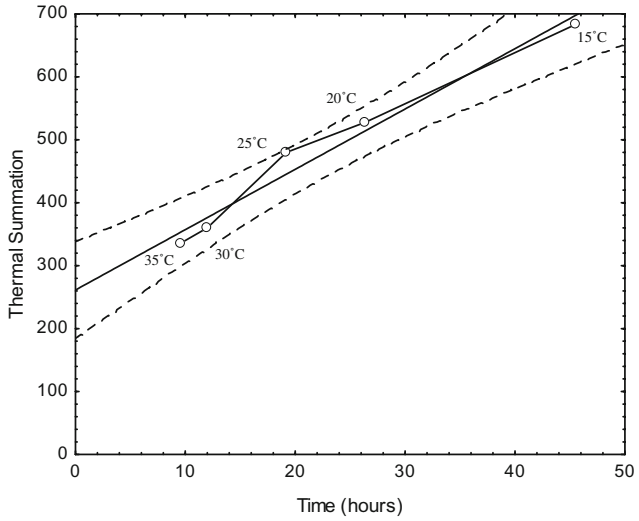
As Dadour et al. [8] pointed out, the length of a maggot is a poor estimator of its physiological or chronological age. This is true of many animals, but some additional factors are evident in *C. albiceps*. Maggots of *C. albiceps* regularly diminish in length, not only when they cease wandering and begin to pupariate but also briefly after each ecdysis. Comparable patterns of fluctuation in mass and length were noted by Wells and LaMotte [44] and Grassberger and Reiter [12], respectively. Our results (Fig. 1) suggest that in conducive environmental conditions, maggots will maximize growth in size to maximize fecundity as adults, as larger females are generally more fecund [34]. When environmental conditions are less favorable, maggots adjust their developmental period in a trade-off between risk of mortality and compromised body size (Fig. 1). Only when environmental conditions are extremely cold do maggots completely prioritize development time over size, resulting in dwarfed adults. In *C. albiceps*, this occurred at temperatures below 20°C (Fig. 1).

Additionally, maggots decrease in length as they enter the wandering phase (see Grassberger et al. [14]: Fig. 2). This can usually be detected and corrected for by examining the crop contents, which are eliminated at the onset of wandering. The practical implication of these physiological phenomena is that there is no simple relationship between size and chronological age in maggots [8]. An isomegalen diagram [12] can capture a great deal of the complexity of the relationship, especially if superimposed on an isomorphen diagram (Fig. 1), and provides a means of estimating postmortem intervals from maggot length. Unfortunately, few of these diagrams are available. For these reasons, we agree that maggot age may not be best estimated from their length given our current knowledge [8, 10].

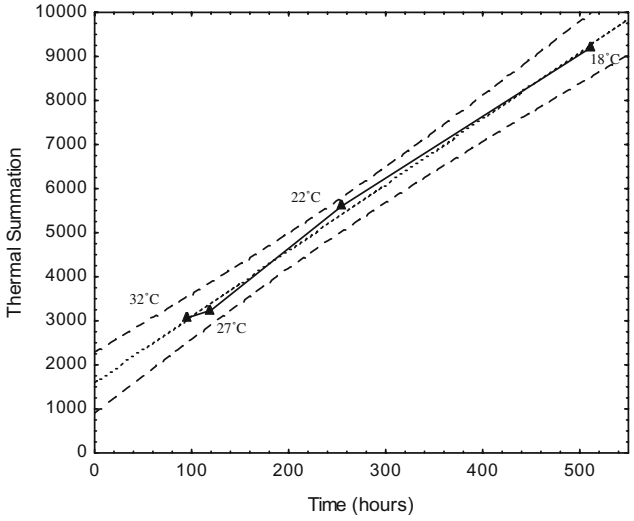
Thermal summation constant (K) and development zero (D_0)

The developmental zeros for the second ecdysis, onset of wandering, onset of pupariation, and eclosion averaged 13.55°C (standard deviation=0.39) and did not differ significantly, with a maximum difference of 0.9°C between the second ecdysis and the onset of wandering. This consistent D_0 value between developmental events is to be expected because the kinetics of metabolism is unlikely to vary between developmental stages in insects [35]. The estimated developmental zero for the first ecdysis was 2.41°C lower than those of the other events, but its accuracy is compromised, as samples of first instar larvae were taken with a

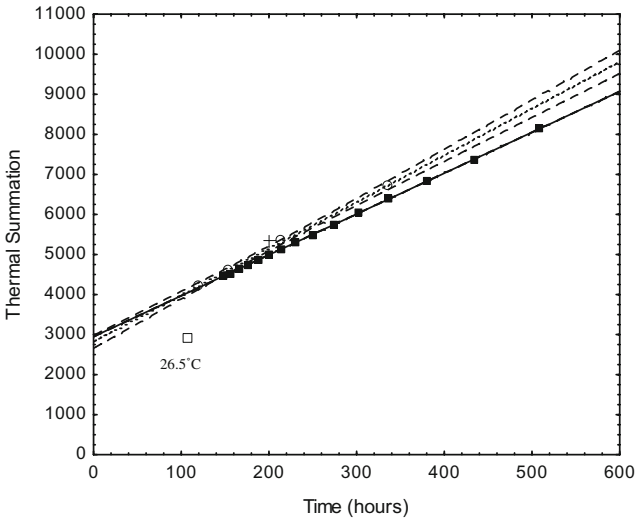
Hatching



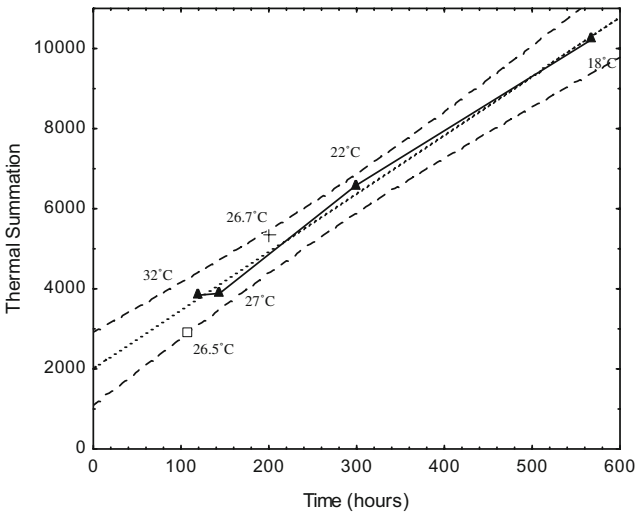
Wandering



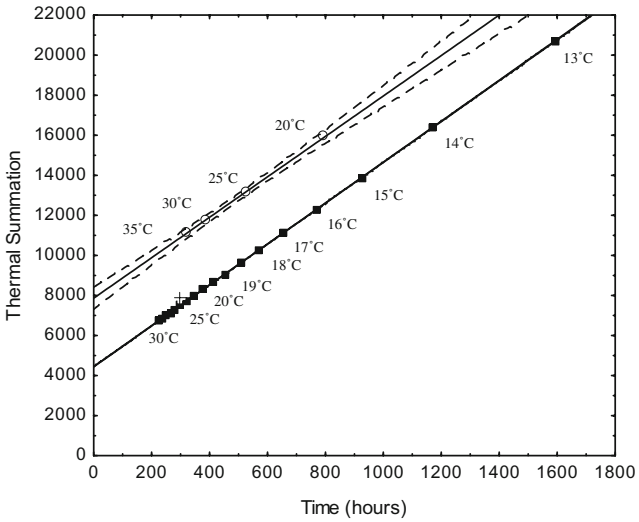
Pupariation



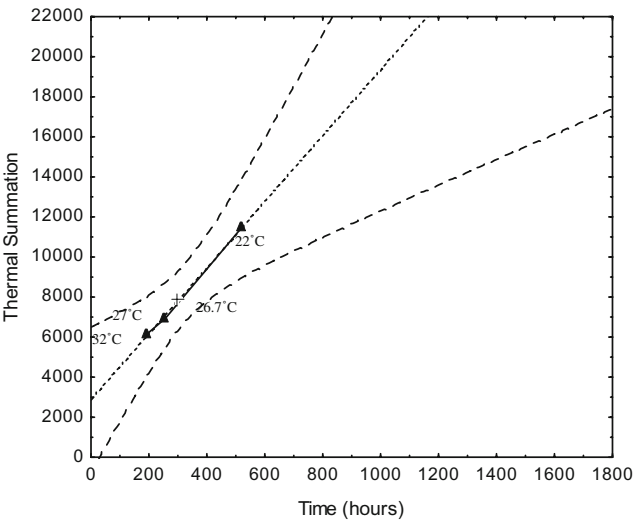
Pupariation



Eclosion



Eclosion



◀ **Fig. 3** S-shaped curves and reduced major axis regression lines used to determine K and D_0 values of *C. albiceps* for hatching, onset of wandering, onset of pupariation, and eclosion. Sources: *open square* Ullyett [40]; *plus symbol* Prins [31];*filled triangle* Queiroz [33]; *filled square* Marchenko [27]; *open circle* Grassberger et al. [14]. *Dotted lines* represent 95% confidence intervals

lower relative temporal resolution than of the other developmental events due to the rapid growth of first instar larvae, particularly at high temperatures. Most published studies sampled at fixed intervals that ranged from 4–12 h (e.g., [12–14, 25, 29, 28]). Bearing the current results in mind, future studies should aim for a relative temporal precision of about 10% of the total duration being measured, which translates into a sampling interval of about every 2 h before hatching, about every 3 h before the first ecdysis, and about every 6 h before the second ecdysis.

The average D_0 and K for *C. albiceps* varied between studies. Reasons for this variation can be attributed to two possibilities, namely differences in rearing conditions, with particular reference to diet of immature stages, or because the populations in each study differed in geographic latitude. Although rearing media are known to affect duration of development (and therefore K) [6, 23, 22], it is still possible to compare D_0 values from different studies that have used different rearing conditions. This is because D_0 is a measure of temperature only and is not affected be variables influencing time, such as rearing media. Because K is a measure of time, the different rearing media used in different studies must be taken into account when comparing K values.

Kaneshraja and Turner [23] tested development of *Calliphora vicina* on liver, lung, heart, brain, and kidney tissue of pigs at 20°C. They found that development rates were significantly slower on liver with an error of up to 2 days (33%) of development when compared to other tissues for the first 6 days. This is presumably because these were the days when the larvae where feeding. However, once the larvae were post-feeding, the error in development reduced to as little as 10%, as all larvae reached pupariation on all rearing media between 9–10 days. Presumably, the error will decrease further on eclosion. Therefore, it is unlikely that rearing media would significantly affect total development time, and because the comparison between studies in this paper are restricted to the post-feeding stages only (pupariation and eclosion), it is unlikely that the diet used by the different studies will significantly affect the comparisons between K values.

If rearing media had a significant effect on K values, we would expect the K values from this study to be most similar to Grassberger et al. [14] as both used liver, and the K values from Marchenko [26] to be most similar to Queiroz [33] as both used meat. However, this is not the case. The K value, for pupariation and eclosion, for this study are closer to Queiroz [33] value than to Grassberger et al. [14] (Table 1; Fig. 1). Therefore, reasons for the varying K values for pupariation and eclosion cannot be attributed primarily to rearing media. An alternative is different geographic populations.

The data also suggest that D_0 and K are inversely proportional and that K is directly proportional to geographic latitude (Fig. 4). The inversely proportional relationship between K and D_0 has been shown in a number of different plant and animal species [2, 5, 17–19, 36–39], including some flies [17, 20], but never demonstrated in species of blowflies. Initially Trudgill and Perry [38] and Trudgill [37] 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. Honêk [17] tested this hypothesis with recalculated K and D_0 values from literature on 335 insect species. He found

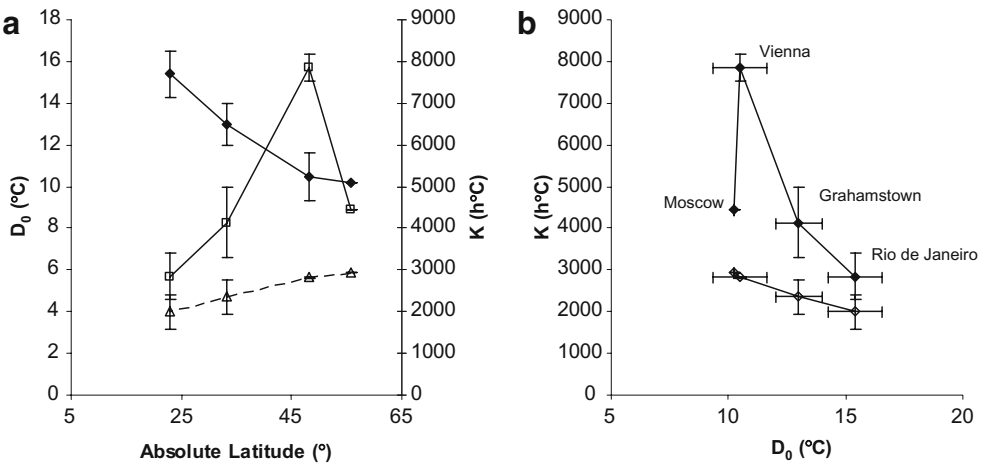


Fig. 4 **a** Relationships between absolute latitude and D_0 (*filled diamonds*), K for pupariation (*open triangles*), and K for eclosion (*open squares*). **b** Relationships between D_0 and K. *Filled symbols* eclosion, *open symbols* pupariation. *Error bars* represent 95% confidence intervals

weak but significant correlations indicating that D_0 was inversely proportional to geographic latitude in all developmental events, including hatching (r^2=0.150), larval growth (r^2=0.142), pupation (r^2=0.040), and eclosion (r^2=0.121). A less obvious relationship existed between K and geographic latitude, although a positive correlation was found for hatching (r^2=0.034). Honêk [17] concluded that a high D_0 and low K are typical thermal characteristics of warm-adapted (tropical) species.

Although our data support these findings, our D_0 exceeded Honêk's [17] data by 1.70–2.82°C for tropical (0–23°N or S) populations, by 0.74–2.82°C for subtropical (24–39°N or S) populations, and by 1.92–2.35°C for temperate (≥40° N or S) populations. Reasons for these differences could be that Honêk [17] did not separate species on eco-physiological criteria, such as seasonality of development in temperate species [20] and size categories, for the analysis.

The positive correlation between K and geographic latitude has often been reported in plants, particularly legumes [1, 7, 32], but rarely in insects [17]. These data (Fig. 3) present evidence that K is directly proportional to geographic latitude. Our data are based on only one or two points for each climatic zone. Additional studies are required, either at alternative latitudes or replicates of these latitudes (Fig. 3) to confirm the pattern. Should these data be obtained, it may be possible to derive a model for the accurate calculation of K and D_0 for *C. albiceps* at any latitude. It is likely that Marchenko's [26, 27] K value for eclosion is an underestimate, on the basis that his estimate of D_0 for pupariation is more or less consistent with monotonic relationships based on the other published studies (Fig. 4).

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