PAPER

PATHOLOGY/BIOLOGY

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Estimating the Preappearance Interval from Temperature in *Creophilus maxillosus* L. (Coleoptera: Staphylinidae)*,†

ABSTRACT: Some carrion insects appear on carcasses late in decomposition. While using these late-arriving taxa to estimate postmortem interval, it is vital to accurately estimate an interval preceding their appearance on a cadaver called the preappearance interval (PAI). This paper tests the possibilities of a PAI estimation from temperature in case of late-arriving, predatory carrion beetle *Creophilus maxillosus*. The relationship between temperature and PAI of adult and larval *C. maxillosus* was modeled using the results of a large-scale experiment on succession in forests of Central Europe. In both stages, PAI was found to be strongly, inversely related to temperature averaged for the duration of PAI. The PAI estimation from mean degree-day accumulations (mDDA), estimated DDA, and "PAI*T*" functions were tested using external successional data. The greatest accuracy of PAI estimates was achieved using an exponential "PAI*T*" function.

KEYWORDS: forensic science, forensic entomology, postmortem interval, degree-days, *Creophilus maxillosus*, validation

There are two approaches to estimate postmortem interval (PMI) from entomological evidence: a development-based approach and a succession-based approach (1–3). A key point of the development-based approach is to age immature insects sampled from a corpse (1–7). This approach is widely used in short PMI cases (particularly with immature blowflies), and it usually results in an estimate of the minimum PMI (2,3,6,7). In case of taxa that colonize carcasses shortly after death (e.g., blowflies), the minimum PMI is a very good approximation of PMI (Fig. 1). However, with insects that start breeding late in decomposition, the minimum PMI is clearly an inaccurate approximation of PMI (Fig. 1). It results from the fact that minimum PMI says nothing about an interval preceding the appearance of a taxon on a corpse. Consequently, to obtain an accurate estimation of PMI, one should estimate not only the development interval but also the preappearance interval (PAI). The estimation of PAI is critically important in case of those insects that colonize carcasses late in decomposition as, for example, most carrion-breeding beetles (8). In some cases, PAI may be much longer than the development interval, and thus, lack of its estimation or an inaccurate estimation may clearly invalidate the resultant PMI (Fig. 1).

While using the succession-based approach in the way proposed by Schoenly et al. (9), after choosing the model of succession and taxa which will define lower (minimum) and upper (maximum) PMI, one has to estimate the values of lower and upper PMI for a given case. The lower PMI is simply the PAI of a first definitive taxon, and the upper PMI is a sum of PAI and the presence interval of a second definitive taxon (Fig. 2). Consequently, the accuracy of lower and upper PMI depends on the accuracy with which PAI of definitive taxa was estimated. Therefore, the estimation of PAI of carrion insects is the essence of the succession-based approach.

Currently, the only way to estimate PAI for most carrion taxa is to use results of experiments on succession. To this end, one has to search for the experiment which closely mirrors the context of the case and then carefully use its results to estimate PAI of a given taxon. Unfortunately, this context-dependent way of PAI estimation is clearly impractical, as it demands a huge body of forensically useful successional data.

Results of recent studies suggest, however, that in some taxa the PAI may be estimated from temperature. Megyesi et al. (10) demonstrated that decomposition of human remains is best modeled as dependent on accumulated temperature. Although this study covered only physical changes in the corpse, its results prompt to speculate that other processes during decomposition (e.g., entomological succession) may also be modeled as dependent on temperature. This hypothesis was supported by work of Michaud and Moreau (11), who demonstrated in some forensically useful insects that their presence on carrion is predictable with respect to temperature accumulations and seasonal effects. Although this study modeled the residency on carrion as dependent on temperature accumulations, its results suggest that the PAI in some carrion insects may also be temperature dependent. This speculation is supported by paper of Matuszewski et al. (12), who found a strong relationship between the time of a taxon appearance on carrion (and consequently PAI) and the onset of bloating in many carrion insects. Because the time necessary for the manifestation of bloating is strongly inversely related to temperature

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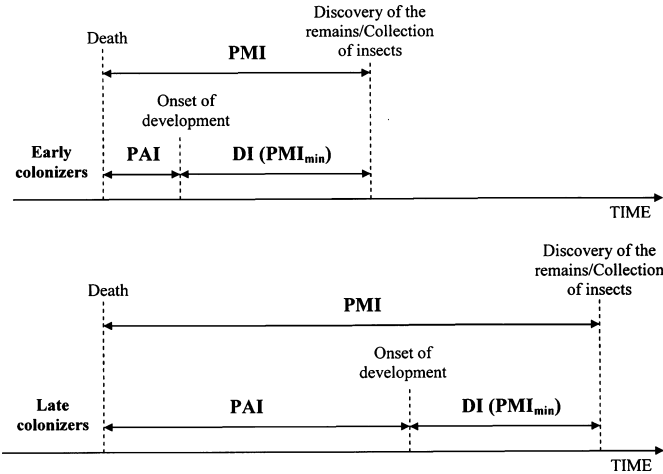
FIG. 1—*Importance of the preappearance interval (PAI) while estimating the postmortem interval (PMI) from the development of early and late colonizers. DI, the development interval; PMImin, minimum postmortem interval.*
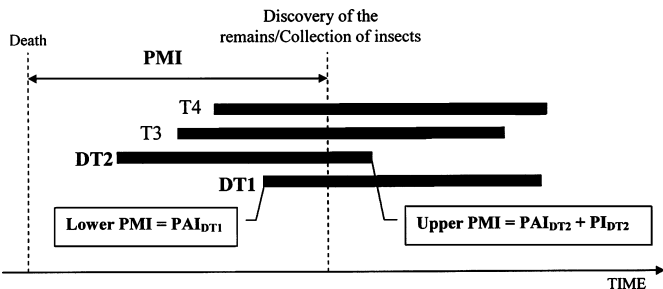

FIG. 2—*Importance of the preappearance interval (PAI) while estimating the postmortem interval (PMI) from the succession of insects. T1–T4, taxa sampled from the remains; DT1, a taxon defining lower PMI; DT2, a taxon defining upper PMI; PI, the presence interval.*

(13), these results suggest that the time in which insect species appear on carrion is strongly related to temperature. Moreover, Matuszewski et al. (14) found that in many carrion taxa seasonal, annual, and environmental differences in appearance time (and consequently PAI) closely mirror corresponding differences in temperature.

All these data prompt to hypothesize that in some carrion insects the PAI is closely related to temperature and may be estimated from temperature in a context-free way. This way of PAI estimation is context-free in this sense that the same model of relationship between PAI and temperature is used in any case irrespective of its context. Obviously within this approach, the context of the case is still clearly important, as it affects, for example, estimation of temperatures to be used in the case. Nevertheless, the estimation of PAI in itself is context-free.

In this paper, I test the possibilities of an estimation of PAI from temperature in adult and larval *Creophilus maxillosus* L. (Coleoptera: Staphylinidae). *C. maxillosus* is a broadly distributed carrion beetle, which repeatedly breeds in carrion and regularly appears late in decomposition (12,14–21). In both feeding stages, it is predatory and feeds on maggots and pupae of flies (22). In the case of adult and larval *C. maxillosus*, strong correlations between the time of their appearance on carrion and the onset of bloating were found (12). Because the time necessary for the onset of bloating is strongly inversely related to environmental temperature (13), these

results suggest that PAI of adult and larval *C. maxillosus* is closely related to temperature and, thus, may be estimated from temperature in a context-free way. Accordingly, here I test the hypotheses that in case of adult and larval *C. maxillosus* a close inverse relationship exists between the temperature of the environment and PAI. Moreover, the nature of the relationship is investigated, degree-day models are constructed, and the accuracy of different methods in estimation of PAI is evaluated.

Materials and Methods

The Relationship Between PAI and Temperature

The relationship was evaluated with data from a forensically oriented experiment on pig carrion decomposition and insect succession in forests of Central Europe (12,14,23). The experiment was conducted in three types of forests (alder forest, hornbeam-oak forest, and pine-oak forest) during spring, summer, and autumn of 2006 and 2007. In total, 36 domestic pig (*Sus scrofa domestica*) carcasses of similar weight (mean = 25.8 kg) were used. Beetles were collected using pitfall traps and manual sampling. Until the end of active decay, sampling was performed daily. Adult and larval *C. maxillosus* appeared within the daily period of sampling in all carcasses. A detailed description of methods may be found in Matuszewski et al. (12,23).

The PAI is an interval from the moment of death until the appearance of the first specimen of a given stage. The relationship between PAI and temperature was tested separately in adult and larval stages. The larval stage was chosen instead of the egg stage, owing to difficulties in sampling eggs of *C. maxillosus* in the field (it oviposits in the soil around the carcass).

In the case of the adult stage I included in the analyses, those carcasses on which at least five specimens had been recorded. It resulted in 32 observations and a PAI range of 2–34 days. In the case of the larval stage, I included in the analyses those carcasses on which at least 10 specimens had been recorded. This gave 29 carcasses and a PAI range of 9–39 days.

Instead of ambient air temperature, I used ground-level temperature, as it better models temperature of the environment where carcasses are exposed on the ground. I decided to use neither the temperature of carcass tissues nor the correction of ground-level temperatures with maggot mass effect. While these temperatures would better model the temperature of the environment as compared to ground-level temperatures, they are closer to temperatures that affect the process producing attractants of *C. maxillosus* (whatever is the process, it certainly acts within a carcass). However, in casework, they are in majority of cases unavailable. Moreover, currently, there is no useful method of correcting ambient air or ground-level temperatures to cover carcass characteristics or maggot mass effect. Consequently, models of relationship between PAI and temperature, other than ambient air or ground level, would be practically useless.

Mean daily ground-level temperatures were obtained from a weather station located about 13 km from the area of the study. They were corrected using the linear regression performed with data from the station and on-site measurements. On-site measurements were taken during every sampling. Moreover, day-long measurements were taken as described in Matuszewski et al. (23). All these data were included in the analyses. After correction, mean daily temperatures were averaged for the duration of PAI. Consequently, in the case of adult *C. maxillosus*, the averaged temperatures ranged from 11.4 to 21.7°C, and in the case of larval *C. maxillosus*, they ranged from 11.8 to 20.1°C.

The relationship between PAI and temperature was evaluated using regression analysis. The linear and exponential [$y = b*\exp(-q*x)$] models were tested. In the case of the exponential model, the Levenberg–Marquardt method of estimation was used. It is a standard algorithm used to estimate parameters of the nonlinear models of regression.

Degree-Day Models

Base temperatures (T_b) were calculated using four methods. Two methods used the x-intercept approach (1/PAI plotted against temperature), the first one in the full temperature range and the second one in the low temperature range (6). Low temperature range was defined as $T < 16°C$. The third and the fourth methods were based on the assumption that T_b is the temperature which results in the lowest variation in degree-day accumulations (DDA) for a given set of field observations (24). The third method used the 15th formula proposed by Yang et al. (24, p. 66) for the least coefficient of variation in DDA. In the fourth method, calculations of DDA for different T_b were performed iteratively. I have started with T_b calculated using the 15th formula of Yang et al. (24) and successively changed it by ±0.1°C. For each T_b, accumulations were worked out and their variation was evaluated. Eventually, the T_b that resulted in the least variation in DDA was found. For all T_b, the variation in DDA was estimated with the coefficient of variation.

Degree-days (DD) were calculated using the formula DD = $T - T_b$, where T is the mean daily ground-level temperature and T_b is a given base temperature. When $T < T_b$, the DD were set to zero. DDA were calculated by adding together all DD for the duration of PAI. To test whether DDA were related to average temperature for the duration of PAI, "DDA*T" scatter plots were made and the relationship was analyzed using linear regression.

Accuracy of Estimations

Three methods of the estimation of PAI were evaluated. The first method uses mean DDA (mDDA). It was tested in four variations differing in the T_b used. The second method uses DDA estimated from equations regressing DDA against temperature. It was also tested in four variations differing in the T_b used. The third method estimates PAI directly from "PAI*T" function. It was tested in two variations, one with a linear function and one with an exponential function. To use the second or third method, one has to estimate mean daily ground-level temperature which will approximate the environmental temperatures present for the duration of PAI in the case of a given corpse. These temperatures are eventually used to estimate DDA as in the case of the second method or to directly estimate PAI as in the case of the third method. To obtain these temperatures for particular carcasses, I have selected from the literature average seasonal PAI of a given taxon in a given biogeographic location or the nearest similar area for which such data have been published. For example, for the European cases, I used data published by Matuszewski et al. (14). Then, for these rough PAIs, daily temperatures were averaged and these temperatures used to estimate DDA (the second method) or PAI (the third method).

Methods of PAI estimation were tested using external data. For this purpose, the carrion succession literature was searched for reports, indicating PAI of adult or larval C. maxillosus with accompanying temperature data. Eventually, 26 carcasses were included in the analyses in the case of the adult stage and eight carcasses in the case of the larval stage (Table 1). Because most sources report only ambient air temperatures, ground-level temperatures were obtained through simple correction. For spring or summer cases, daily ambient temperatures were increased by 0.5°C, whereas for autumn and winter cases, daily ambient temperatures were decreased by 0.3°C. The correction factor was obtained through calculations of average seasonal differences between ambient and ground-level temperatures for the local weather station data. This method of correction only roughly approximates actual ground-level temperatures; however, it was the only way to get more accurate temperatures.

The accuracy of estimations was measured using absolute and relative errors. The following formulae were used:

$$\text{absolute error} = |PAI - ePAI| \text{ and}$$

$$\text{relative error} = \frac{|PAI - ePAI|}{PAI} \times 100\%$$

where PAI is an actual preappearance interval and ePAI is an estimated preappearance interval.

The significance of differences in relative errors of estimates between methods of PAI estimation was evaluated with analysis of variance for repeated measures (rmANOVA) designs. Method of PAI estimation was a repeated factor. For the purpose of multiple pairwise comparisons, the Fisher least significant difference procedure was used.

For all statistical analyses, a 5% level of significance was accepted. Calculations were made using STATISTICA 8.0 (28).

Results

The Relationship Between PAI and Temperature

In both stages, PAI was strongly inversely related to mean daily ground-level temperature averaged for the duration of PAI (Figs 3–4). The exponential models showed better fit than the linear models; however, the difference in variation explained was clearly negligible (below 1%, Figs 3–4).

Degree-Day Models

Base temperature (T_b) resulting in the lowest variation in DDA was 10.8°C in case of the adult stage and 9.5°C in case of the larval stage (Table 2). In case of the larval C. maxillosus, both versions of the x-intercept method (Fig. 5) produced higher T_b resulting in higher variation in DDA (Table 2). As for the adult C. maxillosus, the x-intercept method in the low temperature range (Fig. 6) gave T_b being close to the temperature resulting in the lowest variation in DDA (Table 2). mDDA needed for the appearance of adult C. maxillosus was about 56 DD ($T_b = 10.8°C$) and larval C. maxillosus about 126 DD ($T_b = 9.5°C$) (Table 2). In both stages and with all T_b, a broad range of DDA and a substantial variation in DDA were recorded (Table 2). In case of most T_b, DDA were to some extent related to mean daily ground-level temperatures averaged for the duration of PAI (Figs 7–8).

Accuracy of Estimations

In the case of adult C. maxillosus, method of PAI estimation had a significant effect on the relative error of PAI estimates (rmANOVA, $F_{9,225} = 4.997$, $p < 0.0001$, Fig. 9). In case of larval C. maxillosus, no significant effect was found (rmANOVA, $F_{9,63} = 1.483$, $p = 0.17$, Fig. 9).

TABLE 1—*Data used in the evaluation of accuracy of the preappearance interval (PAI) estimation.*

Source	Stage	PAI (days)	Sampling Resolution	T (°C)	Temperature Data	Geographic Location	Season	Carcass Type
Tantawi et al. (15)	A	4	Daily	23.8*	OS, Av	Alexandria (Egypt)	Spring	Rabbit
	A	11	Daily	16.7*	OS, Av	Alexandria (Egypt)	Autumn	Rabbit
	A	16	Daily	13.3*	OS, Av	Alexandria (Egypt)	Winter	Rabbit
Richards and Goff (16)	A	6	Daily	17.9*	OS, D, G	Hawaii (U.S.A.)	Spring	Pig
	A	1	Daily	29.8*	OS, D, G	Hawaii (U.S.A.)	Summer	Pig
	A	8	Daily	17.9*	OS, D, G	Hawaii (U.S.A.)	Autumn	Pig
Tabor et al. (17)	A	4	Daily	18.8*	S, Av	Virginia (U.S.A.)	Spring	Pig
	A	6	Daily	18.2*	S, Av	Virginia (U.S.A.)	Spring	Pig
	A	3	Daily	23.1*	S, Av	Virginia (U.S.A.)	Summer	Pig
	A	2	Daily	25.0*	S, Av	Virginia (U.S.A.)	Summer	Pig
Reckel and Grunwald (25)	A	6.5	Daily	22.4	OS, D	Munich (Germany)	Summer	Pig
Sharanowski et al. (18)	A	16	Every 2–3 days	15.8*	OS, D, G	Saskatchewan (Canada)	Spring	Pig
	A	24	Every 2–3 days	12.2*	OS, D, G	Saskatchewan (Canada)	Autumn	Pig
	A	24	Every 2–3 days	12.7*	OS, D, G	Saskatchewan (Canada)	Autumn	Pig
Matuszewski et al. (19)	A	6.25	Daily	19.5[†]	S, D	Western Poland	Summer	Pig
	A	5.25	Daily	18.2[†]	S, D	Western Poland	Summer	Pig
	A	4.25	Daily	20.8[†]	S, D	Western Poland	Summer	Pig
Wang et al. (20)	A	2	Daily	22.9*	OS, Av	Southern China	Spring	Pig
	A	1	Daily	34.1*	OS, Av	Southern China	Summer	Pig
	A	4	Daily	22.9*	OS, Av	Southern China	Autumn	Pig
	A	10	Daily	18.6*	OS, D	Southern China	Winter	Pig
Grunwald and Reckel (26)	A	8.5	Every 2 days	17.4	OS, D	Munich (Germany)	Summer	Pig
Prado e Castro et al. (27)	A	7	Daily	19.4*	OS, D	Lisbon (Portugal)	Spring	Pig
	A	6	Daily	20.5*	OS, D	Lisbon (Portugal)	Summer	Pig
	A	9	Daily	17.9*	OS, D	Lisbon (Portugal)	Autumn	Pig
	A	27	Every 2 days	9.8*	OS, D	Lisbon (Portugal)	Winter	Pig
Tantawi et al. (15)	L	28	Daily	13.3*	OS, Av	Alexandria (Egypt)	Winter	Rabbit
Sharanowski et al. (18)	L	32	Every 2–3 days	16.6*	OS, D, G	Saskatchewan (Canada)	Spring	Pig
	L	34	Every 2–3 days	14.7*	OS, D, G	Saskatchewan (Canada)	Spring	Pig
	L	16	Every 2–3 days	21.7*	OS, D, G	Saskatchewan (Canada)	Summer	Pig
Matuszewski et al. (19)	L	12	Daily	19.5[†]	S, D	Western Poland	Summer	Pig
	L	24	Every 3 days	16.8[†]	S, D	Western Poland	Summer	Pig
	L	12	Daily	21.7[†]	S, D	Western Poland	Summer	Pig
Wang et al. (20)	L	28	Daily	20.4*	OS, D	Southern China	Winter	Pig

A, adult stage; L, larval stage; T, daily temperatures averaged for the duration of PAI; OS, on-site measurements; S, local weather station measurements; D, mean daily temperatures; Av, average temperatures for the whole study period; G, temperatures reconstructed from the graph.

*Temperatures corrected with a ground-level temperature correction factor (see in the text).

[†]Ground-level temperatures from the weather station corrected using the linear regression of on-site and station measurements.
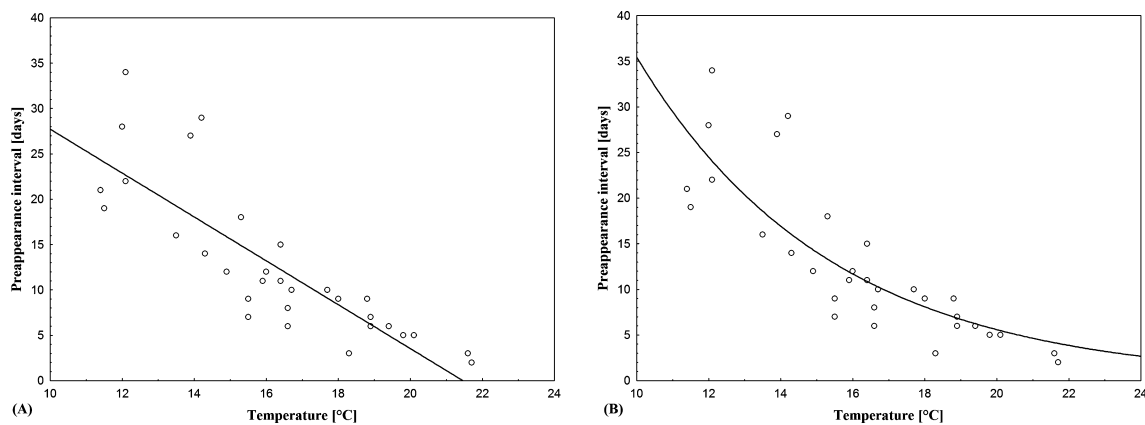

FIG. 3—*Relationship between the preappearance interval (PAI) in adult* Creophilus maxillosus *and mean daily ground level temperatures averaged for the duration of PAI (T). (A) Linear model, PAI = 51.9237–2.4194*T, p < 0.001, r² = 0.6881; (B) exponential model [y = b*exp(−q*x)], PAI = 224.865*exp(−0.184755*T), p = 0.008, r² = 0.6956.*

In both stages, estimations with a direct use of exponential "PAI*T" function resulted in the lowest errors of estimates (Table 3, Fig. 9). The linear "PAI*T" function gave clearly higher errors (Table 3, Fig. 9). In the case of the adult stage, methods employing estimated DDA (eDDA) performed better than methods using mDDA; however, in the larval stage, both approaches gave estimates of similar accuracy (Table 3, Fig. 9). Some DDA methods performed with similar accuracy as compared to the exponential "PAI*T" function, and two of these (eDDA/Yang and eDDA/iteratively) were similarly accurate in both stages (Table 3, Fig. 9). With all methods tested, a broad range of errors and a positively skewed distribution of relative errors were found (Table 3, Fig. 10).
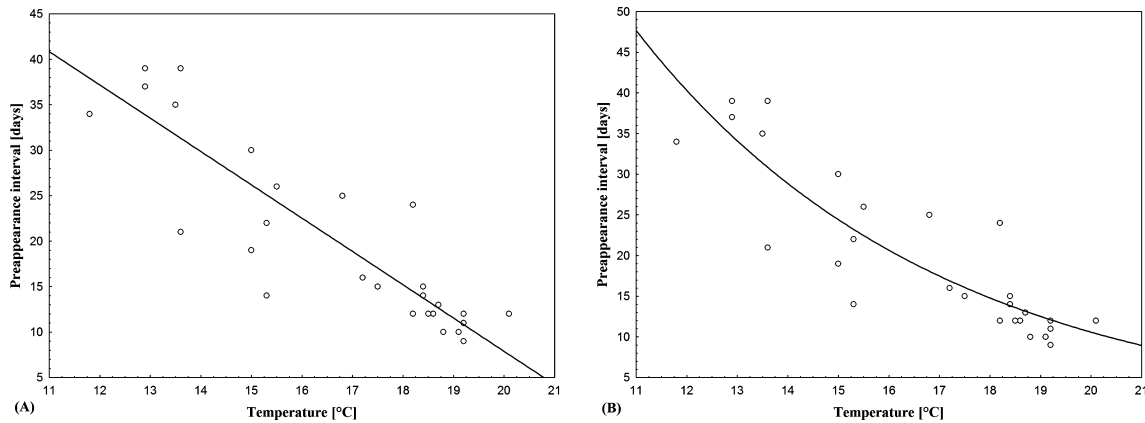
FIG. 4—*Relationship between the preappearance interval (PAI) in larval* Creophilus maxillosus *and mean daily ground level temperatures averaged for the duration of PAI* (T). *(A) linear model,* $PAI = 81.1433 – 3.6631*T$, *p < 0.001,* $r^2 = 0.7854$; *(B) exponential model* $[y = b*exp(–q*x)]$, $PAI = 299.762*exp(–0.167176*T)$, $p < 0.001$, $r^2 = 0.7876$.

TABLE 2—*Base temperatures* (T_b) *and mean degree-day accumulations (DDA) for the preappearance interval in adult and larval* Creophilus maxillosus.

| | | DDA | | |
	T_b (°C)	Mean	Range	Coefficient of Variation in DDA (%)
Adult stage	11.8*	45.7	20.0–78.0	35.47
	10.4[†]	60.6	24.0–104.1	34.47
	9.6[‡]	69.4	25.8–124.5	35.30
	10.8[§]	56.2	23.1–94.8	34.28
Larval stage	12.2*	77.0	35.5–153.8	31.10
	11.7[†]	85.4	42.9–164.4	28.63
	9.3[‡]	129.5	84.7–216.3	24.34
	9.5[§]	125.6	81.8–211.8	24.30

*The *x*-intercept method, full temperature range.
[†]The *x*-intercept method, low temperature range (<16°C).
[‡]The least coefficient of variation in DDA method, 15th equation from Yang et al. (24).
[§]The least coefficient of variation in DDA method, iteratively.

Discussion

The Relationship Between PAI and Temperature

Carrion insects are attracted to carcasses by volatile organic compounds (VOCs) released during decomposition, as was demonstrated for some blowflies or burying beetles which respond to sulfur-containing compounds emitted by a fresh carcass (29–31). VOCs are produced in biological or chemical processes during decomposition. Consequently, it is reasonable to assume that the relationship between PAI and temperature in *C. maxillosus* simply reflects the relationship between the temperature and the process producing VOCs attracting this species. Unfortunately, in case of *C. maxillosus*, the attractants for which this species respond and processes producing these attractants are not known. Actually, it may respond to VOCs being the byproducts of putrefaction, but on the other hand, it may be attracted by some compounds originating from its prey (e.g., larval blowflies).

The relationship between PAI and temperature was close in both adult and larval *C. maxillosus*, which suggests that an interval preceding their appearance on a carcass may be estimated from temperature in a context-free way. Similar results were found for adult and larval *Necrodes littoralis* (32). Both species breed in carrion; consequently, the close relationship between PAI and temperature may be a rule in case of carrion-breeding beetles. Moreover, this paper shows that the predatory taxa may display a satisfactorily close relationship between PAI and temperature.

Similarly, as in the case of *N. littoralis* (32), current results indicate that the relationship between PAI and temperature is exponential in nature. The exponential function better fitted the current data, compared to other popular functions. Moreover, the direct
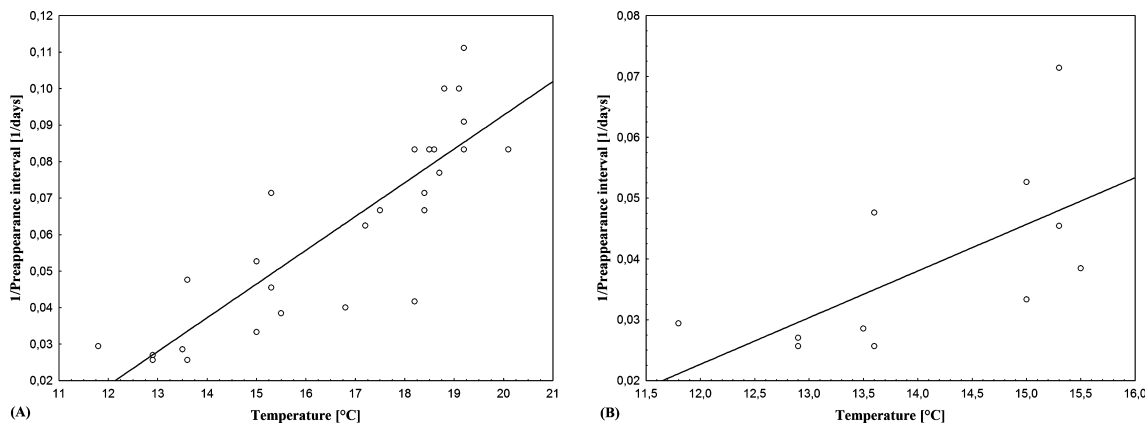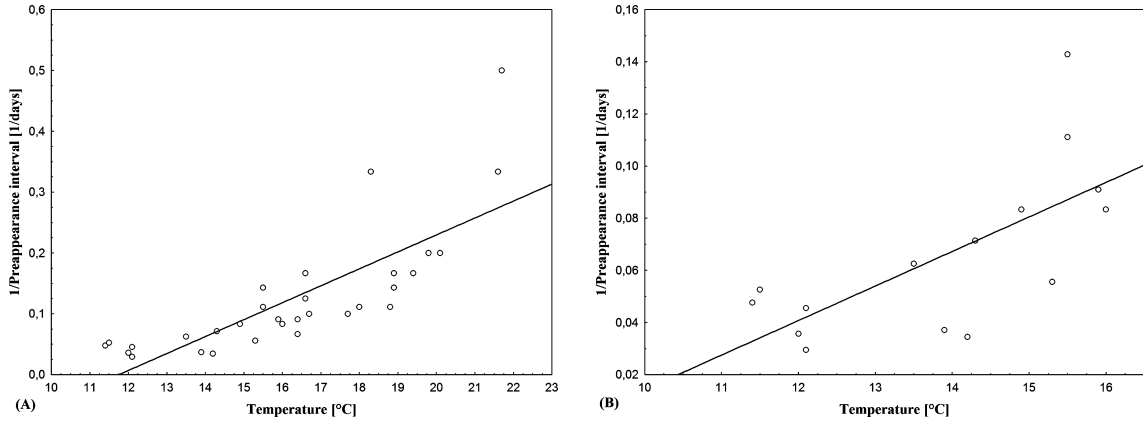

FIG. 5—*Relationship between the transformed preappearance interval (1/PAI) in larval* Creophilus maxillosus *and mean daily ground level temperatures averaged for the duration of PAI* (T). *(A) full temperature range,* $1/PAI = –0.0922 + 0.00924*T$, *x-intercept = 12.2°C; (B) low temperature range* (T < 16°C), $1/PAI = –0.0693 + 0.00767*T$, *x-intercept = 11.7°C.*

FIG. 6—*Relationship between the transformed preappearance interval (1/PAI) in adult* Creophilus maxillosus *and mean daily ground level temperatures averaged for the duration of PAI* (T). *(A) Full temperature range, 1/PAI = −0.3272 + 0.02784*T, x-intercept = 11.8°C; (B) low temperature range (T < 16°C), 1/PAI = −0.1182 + 0.01325*T, x-intercept = 10.4°C.*
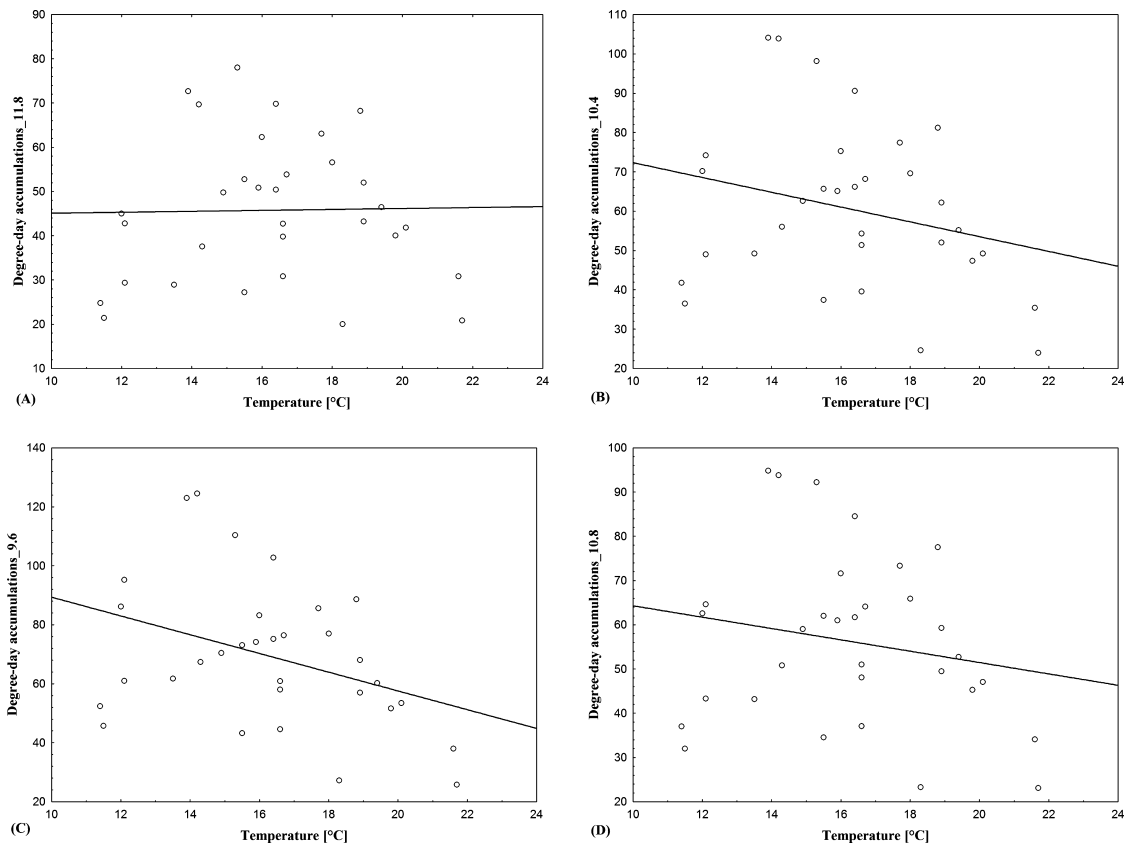
FIG. 7—*Relationship between the degree-day accumulations (DDA) with different base temperatures (T_b) for the preappearance interval (PAI) in adult* Creophilus maxillosus *and mean daily ground level temperatures averaged for the duration of PAI* (T). *(A) DDA for* T_b = 11.8/C, *DDA11.8 = 44.0083 + 0.1069*T, p = 0.92, r^2 = 0.0003; (B) DDA for* T_b = 10.4/C, *DDA10.4 = 91.1467–1.8805*T, p = 0.16, r^2 = 0.0654; (C) DDA for* T_b = 9.6/C, *DDA9.6 = 121.1385–3.1783*T, p = 0.038, r^2 = 0.1356; (D) DDA for* T_b = 10.8/C, *DDA10.8 = 77.1194–1.2828*T, p = 0.3, r^2 = 0.0357.*

estimation of PAI using the exponential "PAI*T" function clearly gave greater accuracy, as compared to the linear "PAI*T" function. The latter resulted mainly from the better performance with cases with very high or very low temperatures.

Degree-Day Models

With all applications of DD, the base temperature is a temperature in which a process being modeled with DD stops.

Accordingly, in the case of the PAI of adult *C. maxillosus*, base temperature may be conceptualized as the temperature in which the process producing attractants of *C. maxillosus* stops. As with other larval species, in case of the PAI of larval *C. maxillosus*, base temperature has no clear biological meaning. It is simply an approximation of three different base temperatures (T_b): T_b for the PAI of adult *C. maxillosus*, T_b for the preoviposition interval (an interval from the appearance of first adult specimen until the onset of oviposition), and T_b for the development of the egg stage.
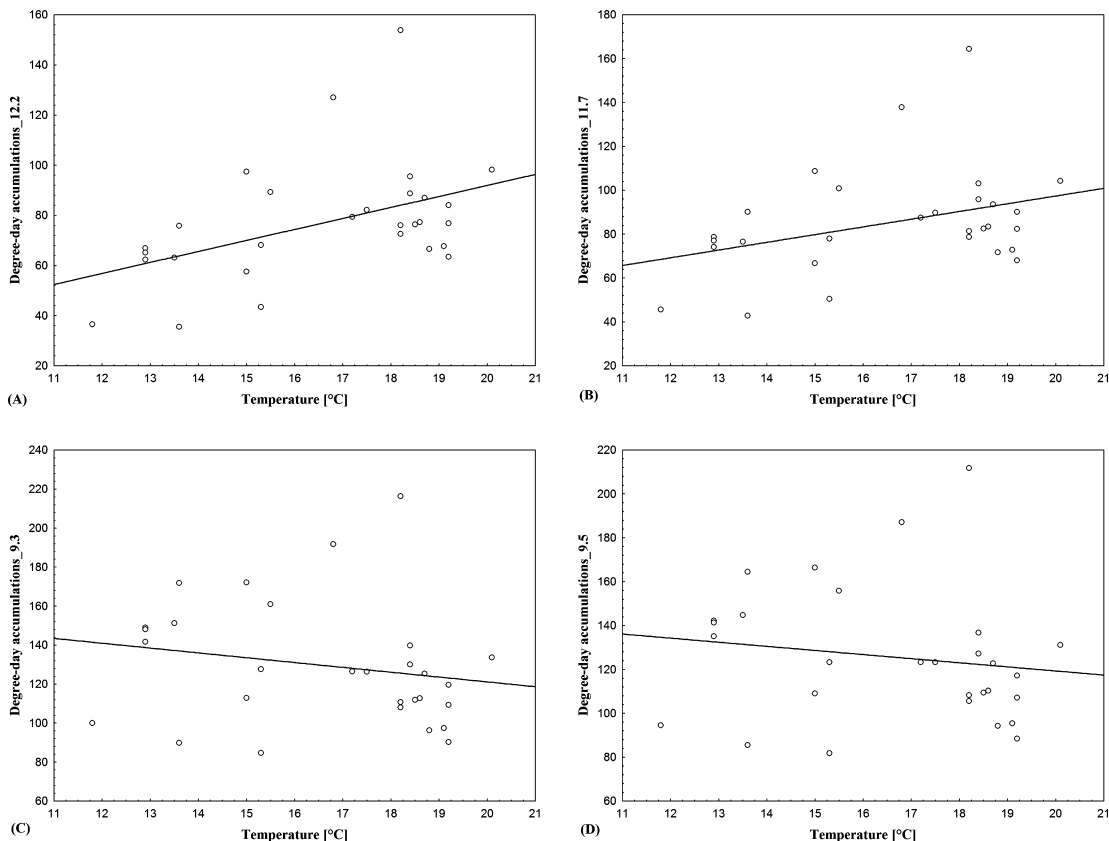
FIG. 8—*Relationship between the degree-day accumulations (DDA) with different base temperatures (T_b) for the preappearance interval (PAI) in larval* Creophilus maxillosus *and mean daily ground level temperatures averaged for the duration of PAI (T). (A) DDA for* $T_b = 12.2/C$, *DDA12.2 = 4.192 + 4.3858*T, p = 0.013, r^2 = 0.2064; (B) DDA for* $T_b = 11.7/C$, *DDA11.7 = 27.0037 + 3.5183*T, p = 0.057, r^2 = 0.1275; (C) DDA for* $T_b = 9.3/C$, *DDA9.3 = 170.674–2.4778*T, p = 0.31, r^2 = 0.0380; (D) DDA for* $T_b = 9.5/C$, *DDA9.5 = 156.7096–1.8706*T, p = 0.43, r^2 = 0.0231.*
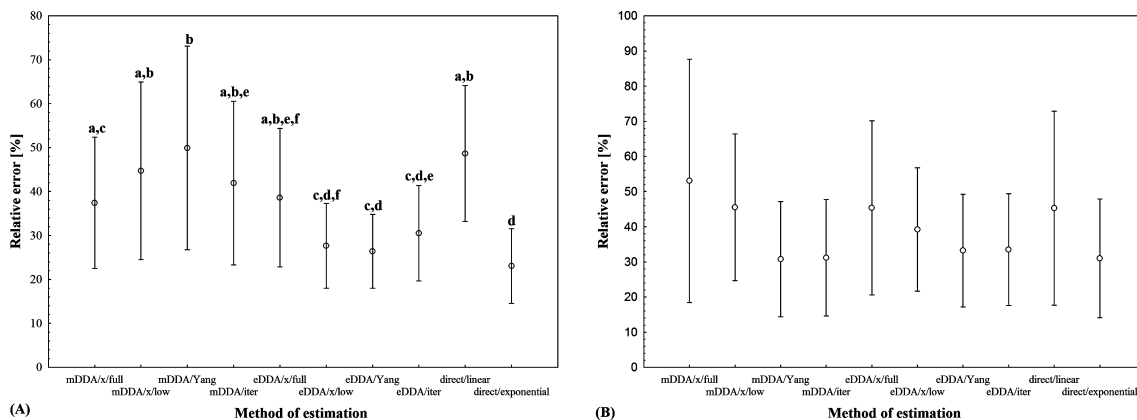

FIG. 9—*The relative error of preappearance interval estimates with different methods of estimation in adult (A) and larval (B)* Creophilus maxillosus. *Vertical bars denote 0.95 confidence intervals. Different letters denote significant differences between methods in pairwise comparisons (p < 0.05). In case of larval* C. maxillosus *no pairwise comparisons were made, as method of estimation had no significant effect on the relative error of estimation. mDDA, mean degree-day accumulations; eDDA, estimated degree-day accumulations; x/full, a base temperature (T_b) determined by using the x-intercept approach in the full temperature range, x/low, T_b determined by using the x-intercept approach in the low temperature range; Yang, T_b determined by using the 15th formula from Yang et al. (24); iter, T_b determined by iterative calculations of DDA for different temperatures.*

Base temperatures produced by the *x*-intercept approach were clearly higher as compared to the ones resulting from the least variation in DDA approach. Similar results were found in the case of adult and larval *N. littoralis* (32). In both species, base temperatures determined using the latter approach are more realistic, and consequently, they seem to better approximate the actual base temperatures as compared to the ones produced by the *x*-intercept approach. Moreover, in the case of larval *C. maxillosus*, estimation of PAI with base temperatures determined using the least variation in DDA approach, resulted in lower errors than estimation with base temperatures determined with the *x*-intercept approach (Fig. 9). These results suggest that in studies on PAI

TABLE 3—*Accuracy of preappearance interval (PAI) estimations with different methods in adult and larval* Creophilus maxillosus.

			Accuracy of Estimations			
			Absolute Error (days)		Relative Error (%)	
	Method of Estimation	N	Mean	Range	Mean	Range
Adult Stage	mDDA/11.8 (x/full)	26	2.62	0.1–17.6	37.4	1–130
	mDDA/10.4 (x/low)	26	2.34	0–11.5	44.7	0–180
	mDDA/9.6 (Yang)	26	2.35	0.3–9.4	49.9	4–210
	mDDA/10.8 (iter)	26	2.33	0–12.8	41.9	0–170
	eDDA/11.8 (x/full)	26	2.64	0.1–17.3	38.6	1–140
	eDDA/10.4 (x/low)	26	2.05	0.1–14	27.7	1–90
	eDDA/9.6 (Yang)	26	1.94	0.2–12.9	26.4	1–80
	eDDA/10.8 (iter)	26	2.16	0–14.8	30.5	0–95
	Directly/linear*	26	2.30	0.1–6.5	48.7	1–100
	Directly/exponential[†]	26	1.36	0.1–3.3	23.1	1–75
Larval Stage	mDDA/12.2 (x/full)	8	13.18	2.4–40.5	53.1	18–145
	mDDA/11.7 (x/low)	8	11.28	2–25	45.5	16–89
	mDDA/9.3 (Yang)	8	7.92	0.2–17.6	30.8	2–63
	mDDA/9.5 (iter)	8	8.02	0–17.7	31.2	0–63
	eDDA/12.2 (x/full)	8	12.06	0.4–28.3	45.4	3–101
	eDDA/11.7 (x/low)	8	10.23	0.4–18	39.2	3–64
	eDDA/9.3 (Yang)	8	8.31	0.6–18.2	33.2	4–65
	eDDA/9.5 (iter)	8	8.39	0.6–18.2	33.5	4–65
	Directly/linear*	8	9.46	2.6–21.6	45.3	16–89
	Directly/exponential[†]	8	7.44	0.8–18.1	31.0	6–65

mDDA, mean degree-day accumulations for a given base temperature; eDDA, estimated degree-day accumulations for a given base temperature; x/full, a base temperature (T_b) determined using the *x*-intercept approach in the full temperature range; x/low, T_b determined using the *x*-intercept approach in the low temperature range; Yang, T_b determined using the 15th formula from Yang et al. (24); iter, T_b determined by iterative calculations of DDA for different temperatures.

*PAI estimated directly using the linear function for relationship between PAI and temperature.

[†]PAI estimated directly using the exponential function for relationship between PAI and temperature.
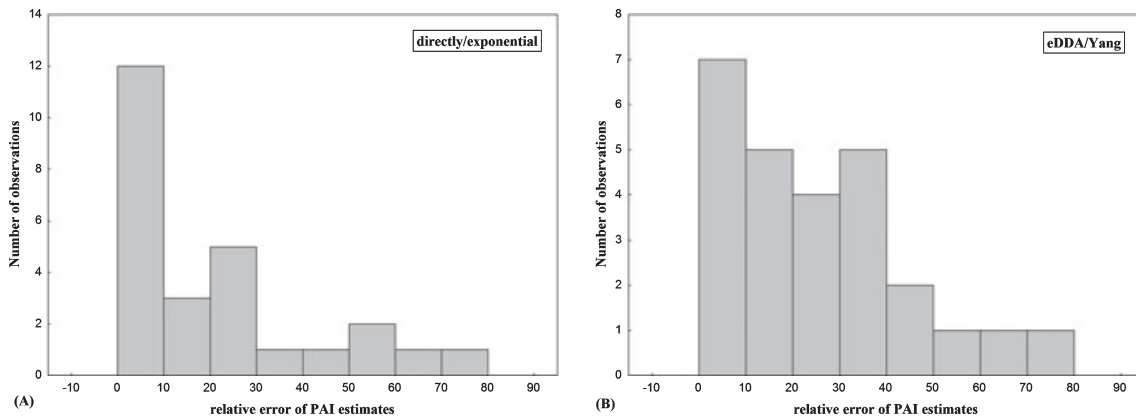

FIG. 10—*The distribution of relative errors in preappearance interval (PAI) estimates of adult* Creophilus maxillosus *in case of the two most accurate methods. (A) Estimation directly by using the exponential "PAI*T" function, (B) estimation with eDDA (estimated degree-day accumulations) and a base temperature determined by using the 15th formula from Yang et al. (24).*

estimation, the *x*-intercept approach generates inadequate base temperatures.

Owing to the broad range and substantial variation in DDA, it was expected that estimation of PAI using the mDDA would result in greater errors than estimation when DDA was calculated using the "DDA*T" functions. Results demonstrated here in case of adult *C. maxillosus* clearly confirm these expectations. Similar results were found in case of adult *N. littoralis* (32). It suggests that the DDA needed for the appearance of adult carrion insects depends on temperature and therefore should be estimated before being used.

Accuracy of Estimations

Lack of significant differences between methods, as recorded in case of larval stage, resulted supposedly from the small size of the sample tested. However, the trends observed are worth discussing, as they were close to a 5% level of significance.

In both stages, PAI estimates reached with the direct use of the exponential "PAI*T" function were, on average, the most accurate of all methods tested. This method performed very well also in case of *N. littoralis* (32). Accordingly, it should be considered equivalent to or even better than the DDA approach. However, it

needs further refinement and, in particular, a more accurate way of determining the average temperature used to obtain a PAI would be essential.

Similar to results achieved for *N. littoralis* (32), estimation of PAI using the eDDA resulted in lower errors as compared to that from the use of mDDA. Therefore, the former approach may be considered superior to the latter.

For all methods, errors are apparently overestimated owing to the weaknesses of the validation procedure used. The procedure was a meta-analysis of successional data, and quite frequently, these data were collected or reported in a way which may have caused substantial inaccuracies (Table 1). For example, in some experiments, the sampling was performed every second day or every third day (Table 1), which caused inaccuracies in PAI determinations and may have increased errors in PAI estimates during the current validation. Moreover, many papers reported temperature data from the weather station, and quite often, only average temperatures for the study period were included (Table 1). Even taking the readings from the graphs with temperature data, owing to the poor resolution of original figures, may have caused some inaccuracies and some overestimation of the errors reported here.

As expected, the distribution of relative errors was positively skewed. However, the most accurate methods had surprisingly high number of estimates with very low errors (Fig. 10). It strongly suggests that the overall accuracy of the best methods is higher and that with better validation data, methods of PAI estimation would perform much better.

Despite the weaknesses of the validation procedure, some methods performed surprisingly well. Because the validation data were collected in experiments with different designs, in different seasons and habitats (Table 1), results of the validation study indicate that models of the "PAI*T" relationship and some methods of PAI estimation are fairly robust and will work in a context-free way. Moreover, successional data used in the current validation were collected in different geographic areas (Table 1). Thus, it is reasonable to speculate that models reported here may give accurate predictions of PAI for adult and larval *C. maxillosus* from different geographic populations.

Self-Critique

Lack of All Day-Long, On-Site Measurements of Temperature—The relationship between PAI and temperature was modeled with data from a local weather station, as no 24-hour on-site measurements were available. Although the station data were corrected to cover microclimatic conditions of particular sites, the whole procedure must have resulted in some inaccuracies of the temperatures used.

Daily Frequency of Sampling—Data on PAI used to model the relationship between PAI and temperature were collected using daily sampling of insects. Adult *C. maxillosus* during very hot weather may appear on carrion even after 2–3 days of decomposition (14). With such an early appearance, daily sampling causes inaccuracies of PAI determinations. The current model covers three such observations.

Acknowledgments

References

1. Catts EP, Goff ML. Forensic entomology in criminal investigations. Ann Rev Entomol 1992;37:253–72.
2. Wells JD, LaMotte LR. Estimating the postmortem interval. In: Byrd JH, Castner JL, editors. Forensic entomology. The utility of arthropods in legal investigations. Boca Raton, FL: CRC Press, 2001;263–85.
3. Amendt J, Campobasso CP, Gaudry E, Reiter C, LeBlanc H, Hall M. Best practice in forensic entomology. Int J Leg Med 2007;121:90–104.
4. Reiter C. Zum Wachstumsverhalten der Maden der blauen Schmeissfliege *Calliphora vicina*. Z Rechtsmed 1984;91:295–308.
5. Marchenko MI. Medicolegal relevance of cadaver entomofauna for the determination of the time of death. Forensic Sci Int 2001;120:89–109.
6. Higley LG, Haskell NH. Insect development and forensic entomology. In: Byrd JH, Castner JL, editors. Forensic entomology. The utility of arthropods in legal investigations. Boca Raton, FL: CRC Press, 2001;287–302.
7. Villet MH, Richards CS, Midgley JM. Contemporary precision, bias and accuracy of minimum post-mortem intervals estimated using development of carrion-feeding insects. In: Amendt J, Campobasso CP, Goff ML, Grassberger M, editors. Current concepts in forensic entomology. Dordrecht, Germany: Springer, 2010;109–38.
8. Midgley JM, Richards CS, Villet MH. The utility of coleoptera in forensic investigations. In: Amendt J, Campobasso CP, Goff ML, Grassberger M, editors. Current concepts in forensic entomology. Dordrecht, Germany: Springer, 2010;57–68.
9. Schoenly K, Goff ML, Early M. A BASIC algorithm for calculating the postmortem interval from arthropod successional data. J Forensic Sci 1992;37:808–23.
10. Megyesi MS, Nawrocki SP, Haskell NH. Using accumulated degree-days to estimate the postmortem interval from decomposed human remains. J Forensic Sci 2005;50:618–26.
11. Michaud JP, Moreau G. Predicting the visitation of carcasses by carrion-related insects under different rates of degree-day accumulation. Forensic Sci Int 2009;185:78–83.
12. Matuszewski S, Bajerlein D, Konwerski S, Szpila K. Insect succession and carrion decomposition in selected forests of Central Europe. Part 2: Composition and residency patterns of carrion fauna. Forensic Sci Int 2010;195:42–51.
13. Korshunov NV, Shved EF, Novikov PI, Vlasov AU, Natcentov EO, Chelyabinsk M. Possibilities of estimation of the time interval necessary for the development of putrefactive manifestation in the corpse. Forensic Sci Int 2003;136:223–4.
14. Matuszewski S, Bajerlein D, Konwerski S, Szpila K. Insect succession and carrion decomposition in selected forests of Central Europe. Part 3: Succession of carrion fauna. Forensic Sci Int 2011;207:150–63.
15. Tantawi TI, El-Kady EM, Greenberg B, El-Ghaffar HA. Arthropod succession on exposed rabbit carrion in Alexandria, Egypt. J Med Entomol 1996;33:566–80.
16. Richards EN, Goff ML. Arthropod succession on exposed carrion in three contrasting tropical habitats on Hawaii island, Hawaii. J Med Entomol 1997;34:328–39.
17. Tabor KL, Brewster CC, Fell RD. Analysis of the successional patterns of insects on carrion in Southwest Virginia. J Med Entomol 2004;41:785–95.
18. Sharanowski BJ, Walker EG, Anderson GS. Insect succession and decomposition patterns on shaded and sunlit carrion in Saskatchewan in three different seasons. Forensic Sci Int 2008;179:219–40.
19. Matuszewski S, Bajerlein D, Konwerski S, Szpila K. An initial study of insect succession and carrion decomposition in various forest habitats of Central Europe. Forensic Sci Int 2008;180:61–9.

20. Wang J, Li Z, Chen Y, Chen Q, Yin X. The succession and development of insects on pig carcasses and their significances in estimating PMI in south China. Forensic Sci Int 2008;179:11–8.

21. Özdemir S, Sert O. Determination of Coleoptera on carcasses in Ankara province, Turkey. Forensic Sci Int 2009;183:24–32.

22. Koch K. Die Käfer Mitteleuropas. Ökologie 2. Krefeld, Germany: Goecke & Evers, 1989.

23. Matuszewski S, Bajerlein D, Konwerski S, Szpila K. Insect succession and carrion decomposition in selected forests of Central Europe. Part 1: Pattern and rate of decomposition. Forensic Sci Int 2010;194:85–93.

24. Yang S, Logan J, Coffey DL. Mathematical formulae for calculating the base temperature for growing degree days. Agric For Meteorol 1995;74:61–74.

25. Reckel F, Grunwald J. Studies on the arthropod succession in the city centre of Munich (Germany) [abstract]. Proceedings of the 5th Annual Meeting of the European Association for Forensic Entomology; 2007 May 2–5. Brussels, Belgium: European Association for Forensic Entomology, 2007;71.

26. Grunwald J, Reckel F. A comparative study on the arthropod succession on dressed and undressed pig carrion in the city of Munich (Germany) [abstract]. Proceedings of the 7th Annual Meeting of the European Association for Forensic Entomology; 2009 June 9–12. Uppsala, Sweden: European Association for Forensic Entomology, 2009;46.

27. Prado e Castro C, Garcia MD, Serrano A, Gamarra P, Outerello R. Seasonal activity of Staphylinidae (Coleoptera) carrion communities from Lisbon, Portugal [abstract]. Proceedings of the 8th Annual Meeting of the European Association for Forensic Entomology; 2010 Sept 8–11. Murcia, Spain: European Association for Forensic Entomology, 2010;62.

28. StatSoft, Inc. STATISTICA. (data analysis software system), version 8.0, 2009, http://www.statsoft.com.

29. Stensmyr MC, Urru I, Collu I, Celander M, Hansson BS, Angioy AM. Rotting smell of dead-horse arum florets. Nature 2002;420:625–6.

30. Kalinová B, Podskalská H, Růžička J, Hoskovec M. Irresistible bouquet of death—how are burying beetles (Coleoptera: Silphidae: *Nicrophorus*) attracted by carcasses. Naturwissenschaften 2009;96:889–99.

31. Podskalská H, Růžička J, Hoskovec M, Šálek M. Use of infochemicals to attract carrion beetles into pitfall traps. Entomol Exp Appl 2009;132:59–64.

32. Matuszewski S. Estimating the pre-appearance interval from temperature in Necrodes littoralis L. (Coleoptera: Silphidae). Forensic Sci Int 2011;212:180–88.

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