

# Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae)

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**Abstract:** Following individual development by means of the 'sandwich method' the duration of egg, larval, and pupal stages, as well as of adult maturation feeding of the spruce bark beetle (*Ips typographus*) was measured at constant temperatures in the range between 12° and 33°C. At 20°C complete development from egg to adult emerging from pupa averaged 29 days. The proportion of the duration of larval development relative to total preimaginal development increased with temperature. Developmental rates, i.e. the speed of development increased linearly with temperature in a range between 15° and 25°C. Based on linear regressions, lower developmental thresholds were calculated to be 10.6°C (eggs), 8.2°C (larvae), 9.9°C (pupae), and 8.3°C (preimaginal development egg to pupa), respectively. Differing heat sums reported in the literature matched ours when recalculated with our developmental thresholds. A nonlinear model (Logan/Lactin) was fitted to the data which allowed to describe development in the entire temperature range. It further permits to identify lower and upper ( $\approx 40^\circ\text{C}$ ) developmental thresholds as well as optimum temperatures (30–33°C) of the instars.

## 1 Introduction

Following the severe storms in Central Europe at the beginning of this decade the eight-spined spruce bark beetle (*Ips typographus* (L.)) has again attracted increased attention. Abundant breeding facilities in wind thrown logs and favorable subsequent weather conditions gave rise to a long lasting outbreak of this bark beetle (WULF and KEHR, 1991). This led to tremendous additional damage by attack of living spruce trees (*Picea abies* (L.) Karst.). The increased attention to this insect revealed basic gaps in the knowledge of its biology. While the influence of temperature as the key environmental factor acting on development is well documented for most important agricultural pests, such information on *I. typographus* for some reason is very sparse. The most extensive, analytical studies were done by ANNILA (1969) and recently by COELN et al. (1996) while a number of other investigations describe, partly in a mere qualitative way, population development under field conditions (MERKER, 1951; WILD, 1953; ABGRALL and JUVY, 1993). Others deal with activity thresholds and swarming temperatures of adult beetles (VITÉ, 1952; LOBINGER, 1994).

Temperature is the main driving force in simulation models of the population dynamics. The aim of this study was to obtain reliable quantitative data on the influence of temperature on immature development of *I. typographus* in view of a future comprehensive model on its population dynamics. Moreover, such data form the basis of risk assessment of outbreaks and their perspectives. Particularly in subalpine forests of the Lower Alps information on the potential number of generations is crucial.

## 2 Materials and methods

### 2.1 Mass rearing

Starting out from teneral beetles collected from a naturally infested spruce tree a mass rearing of *I. typographus* was operated during the experiments. One-meter bolts of spruce trees of 20–30 cm diameter cut some 1–2 months before were placed in a rearing cage (240 × 100 × 80 cm) consisting of screen wire and a Plexiglas front pane. Rearing conditions were at 28°C and 80% rh and a photoperiod of 16:8 L:D. After each generation which lasted approx. 3 weeks fresh bolts were supplied for new colonization. After one week the old logs were removed. Under the above described rearing conditions fungi posed no problems, however predatory gamasid mites (e.g. *Dendrolaelaps armatus*) were quite abundant.

### 2.2 Sandwich construction

The cryptic living and the necessity of following the development of single individuals from egg deposition to emergence of the teneral beetles required a rearing device which allowed easy visual observation of the instars. A modified bark sandwich was chosen based on a technique described for various bark beetle species by e.g. HOPPING (1961), BALOGUN (1969), and KINN and MILLER (1981). Spruce trees of 25–35 cm diameter were felled 2–4 weeks before the start of the experiments. This allowed the phloem to slightly dry up thus reducing resin pressure. Qualitatively inferior bark from trees felled in September/October was avoided (FÜHRER, 1981). Bark pieces of approx. 40 × 25 cm size were thoroughly peeled from the logs and clamped in the sandwich device depicted in fig. 1. It consisted of two Plexiglas panes of 35 × 20 × 0.6 cm. The cover edges were reinforced by Plexiglas strips of 1 cm thickness. The gauze covered aerating holes were 2.5 cm in diameter. A 1 cm piece of plastic tube attached to the 1 cm hole in the pane center allowed the introduction of the parental beetles.

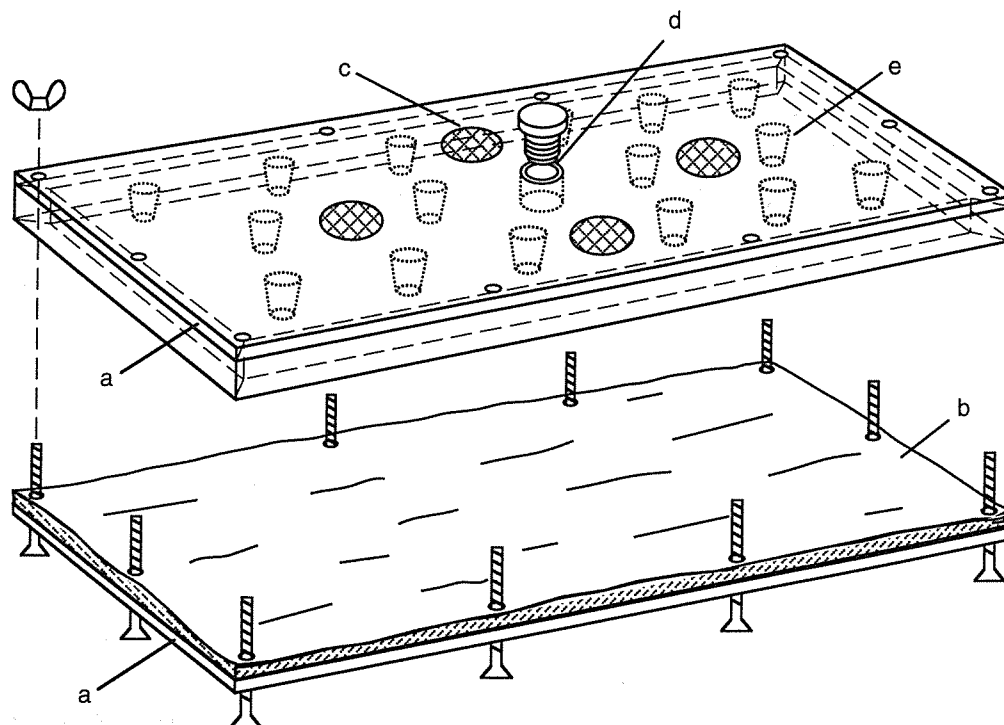


Fig. 1. "Sandwich" device for rearing *I. typographus*; a = Plexiglas pane, b = bark with phloem side down, c = aerating hold, d = entrance tube, e = rubber stopper

Rubber stoppers of 1.2 cm length were glued to the lower pane surface in order to prevent the bark from warping. The sandwiches were evenly and firmly bolted together to make sure that the phloem of the whole bark piece was in close contact with the bottom pane. Otherwise the larvae would leave their galleries. The protruding parts of the bark were cut off and the sandwich sides sealed with adhesive tape. This device permitted adult breeding and juvenile development. Prior to preparing a bark sandwich the Plexiglas panes were disinfected with alcohol.

### 2.3 Experimental procedure

Newly emerged, flight experienced beetles were collected from the mass rearing. They were sexed according to their pronotal hair bristles (SCHLYTER and CEDERHOLM, 1981). Every sandwich was colonized at the entrance tube with one male. During max. two days the males were allowed to excavate the nuptial chambers. Upon completion of the chambers (visible at bottom pane) the sandwiches were exposed to colonization by females in the rearing cage. Exposure time had to be kept short (typically < 5 hours) to prevent entry of too many females. This mate finding process happened at 28°C. As soon as two or more beetles were visible in the nuptial chamber the respective entrance tubes were plugged with a plastic stopper. The sandwiches were transferred to the experimental temperatures immediately after the beginning of maternal gallery construction. Obviously, these first short segments were discarded from the data analysis.

Six temperature regimes were tested: 12°, 15°, 20°, 25°, 30°, and 33°C. For most regimes two separated experiments were conducted. The sandwiches were placed in controlled-temperature cabinets with open water trays to provide sufficient humidity (60–75%). No light was supplied. At the beginning the sandwiches were placed topside up to prevent the parental beetles from falling out of the entrance holes. After the appearance of the first larvae the sandwiches were turned over to keep the larvae in their galleries. When checking the development of

the brood an overhead transparency was placed on the upside down sandwich. The daily increments of the processing maternal galleries were traced on the transparency with pens of different colors, one color for each day. The eggs found in the maternal galleries were considered to be deposited at the same day as the excavation of the respective gallery increment. The duration of the egg stage was estimated as the temporal difference between construction date of the gallery increment and the detection of the neonate larva. Similarly, the expanding larval galleries were traced with different pen colors for each larva. The development stage (egg, larva, pupa, teneral beetle) of each individual was noted daily except for the 33°C treatment with half-day intervals. This enabled us to keep temporal track of the development of each single individual through all stages.

For measuring the period of maturation feeding, emerged beetles were transferred to Petri dishes of 5.5 cm diameter containing equally sized bark disks. Most of the beetles immediately bored into the phloem layer and started/continued their maturation feeding. This period was considered terminated when the beetles left the bark and reappeared at the surface. Newly emerged females were immediately able to mate and oviposit (without flying!), thus proving their maturity. The disks were checked daily.

### 2.4 Analytical methods

Analysis of variance revealed that the different experiments of the same temperature regime did not differ, thus in the statistical analyses data of the same treatment were pooled. All analyses are based on the stage data of one individual as a replicate. Where appropriate means were analyzed by ANOVA ( $\alpha = 0.05$ ) using Data Desk<sup>®</sup> software.

#### 2.4.1 Linear model

Assuming a linear relationship between developmental rate and temperature in a restricted temperature range the lower

developmental thresholds were estimated (CAMPBELL et al., 1974). They were based on the temperature treatments 15°, 20°, and 25°C. In the case of maturation feeding it was based on 20° and 25°C. Straight lines were fitted using weighted least squares analysis (DRAPER and SMITH, 1981). In order to estimate the corresponding weights, for each instar the variance of the observations ( $s^2$ ) was plotted against temperature, and quadratic regressions were fitted to these data points. The values of the regression equations at the treatment temperatures represented the estimates of the variances ( $s_c^2$ ). The inverse of  $s_c^2$  was used as instar specific weight  $\bar{w}_j$  for each data point in the final regression analysis. From the regression

$$r(T) = a + b \cdot T \quad (1)$$

where  $r(T)$  = developmental rate and  $T$  = temperature, the linear regression based developmental threshold ( $DT_{LR}$ ) for each instar was estimated by extrapolating the regression line to  $r = 0$  as

$$DT_{LR} = -\frac{a}{b} \quad (2)$$

The average thermal sum  $K$  required to complete the development was calculated as the reciprocal value of the slope  $b$  of the linear regression line (CAMPBELL et al., 1974)

$$K = 1/b \quad (3)$$

According to CAMPBELL et al. (1974) the standard error  $SE$  of  $DT_{LR}$  can be approximated as

$$SE_{DT_{LR}} = \frac{\bar{r}}{b} \cdot \sqrt{\frac{s^2}{N \cdot \bar{T}^2} + \left(\frac{SE_b}{b}\right)^2} \quad (4)$$

and the standard error of  $K$  as

$$SE_K = \frac{SE_b}{b^2} \quad (5)$$

where:  $\bar{r}$  = sample mean,  $s^2$  = residual mean square of  $r$  (regression),  $N$  = number of observations,  $SE_b$  = standard error of the slope  $b$ .

A two sample t-test (two-tailed hypothesis) was used to test for significant differences between threshold temperatures of individual instars and the overall preimaginal development.

#### 2.4.2 Nonlinear model

The relationship between developmental rate and temperature across the whole range of naturally occurring temperatures is nonlinear. In order to describe this relation and to assess the upper threshold for development we used the Logan model (LOGAN et al., 1976) with the modifications described by LACTIN et al. (1995). Basically, this modification yields better fits at low temperatures. The model is

$$r(T) = e^{\alpha T} - e^{[\alpha T_{max} - (T_{max} - T) \beta] + \gamma} \quad (6)$$

After setting the first derivative of (6) equal to zero the optimum temperature for development  $T_o$  can be calculated:

$$T_o = T_{max} - \frac{\beta \cdot \ln(\alpha \cdot \beta)}{\alpha \cdot \beta - 1} \quad (7)$$

The parameters ( $\alpha, \beta, \gamma$ ) of the Logan/Lactin model were estimated by weighted least square regression using Systat<sup>®</sup> software package.

## 3 Results

### 3.1 Developmental times

In the temperature range between 15° and 30°C developmental data could be obtained for all preimaginal instars of *I. typographus* (table 1). In this range average duration of the egg stage was between 3 and 12 days, that of larvae between 11 and 30 days, and the pupal stage lasted 2 to 11 days, slightly shorter than the embryonic one. At high temperatures such as 30°C total preimaginal development was completed in less than 2.5 weeks. The immobile stages were more pushed by higher temperatures than active stages. The acceleration factor between 15° and 30°C was higher in the immobile stages (eggs: 4.2, pupae: 4.5) than in the active larval stage (2.7). The respective factor for the total development from egg to pupa was 2.8 and was obviously dominated by the long-lasting larval stage.

Relative duration of the larval instar was approx. 60% of the total preimaginal development, that of eggs and pupae amounted to about 20% each (fig. 2). The proportions of the instar duration were temperature dependent. With rising temperatures the relative duration of the active larval stage increased while the proportion of both the inactive egg and pupa stages declined. Primarily in the 30°C treatment the proportions differed significantly from the lower regimes, particularly for the larvae and pupae.

The duration of maturation feeding (table 1) could only be assessed for three temperatures. The acceleration factor between the low and the high temperature treatments was 1.5, thus corresponding more to the analogous ratio of the likewise active larval stage (1.6) than to that of the immobile stages (2.1–2.5). In all temperature treatments the proportion of maturation feeding to total immature development (egg to maturity) was 37–39%. At temperatures  $\leq 15^\circ$  and  $\geq 33^\circ$  no maturation feeding could be measured.

Preliminary experiments at 10° and 35°C showed that at these temperatures development was too strongly impaired to yield reliable results. At 12°C data could be gathered only for embryonic development which lasted more than 3 weeks. Larval development was not possible in this experimental setup (desiccation of the bark, fungi). Similarly, at 33°C dependable data could only be collected for the egg stage which lasted roughly as long as at 30°C. For the other instars sample sizes remained too small to give meaningful results. Nevertheless, the corresponding data are listed in table 1 as informative clues. Supplementary experiments on entire bolts showed that at temperatures of 5° and 40°C no development occurred.

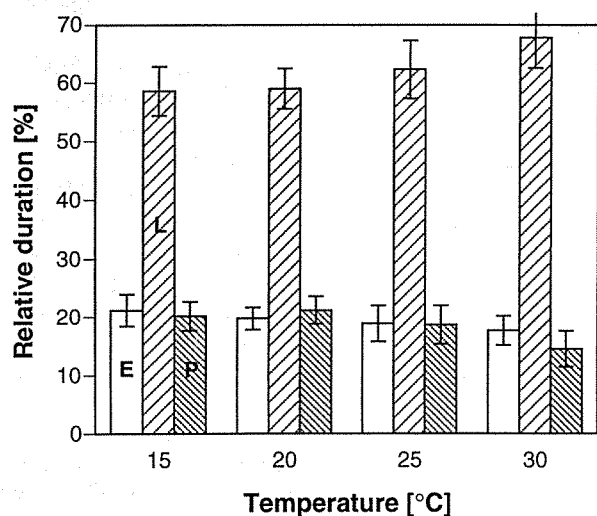
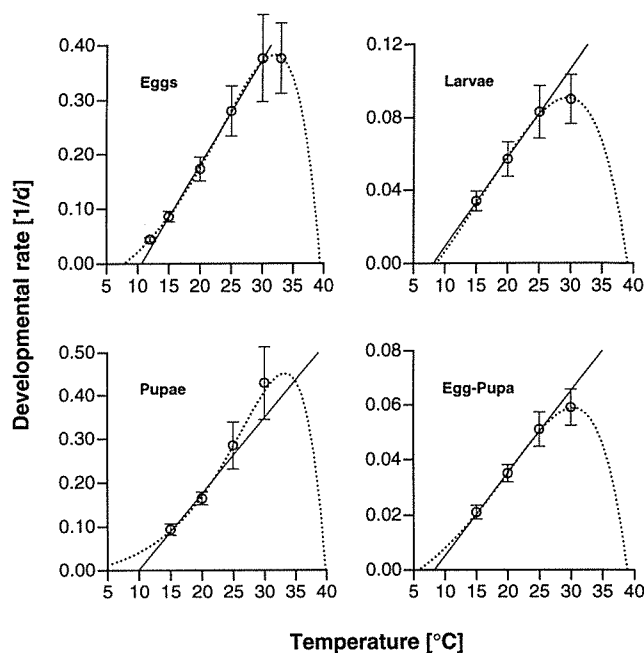
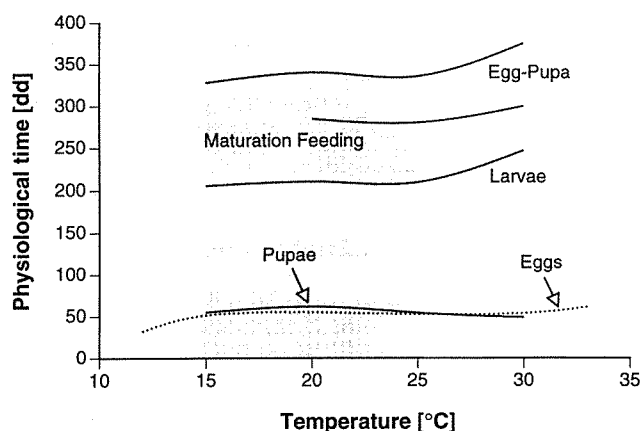
### 3.2 Developmental thresholds and heat sums

The developmental rates of the instars, i.e. the proportion of development completed each day at a given temperature are listed in table 1 as well in fig. 4. From these data the effect of temperature on developmental rates was assessed by linear regression analysis, based on the developmental rates in the linear range of this relation. The parameters of the equations are indicated in table 2. The high correlation coefficients suggest a

**Table 1.** Duration of development and corresponding rates ( $1/\text{duration}$ ) of *I. typographus* at constant temperatures

Temperature	Eggs		Larvae		Pupae		Egg-Pupa		Maturation feeding	
	M $\pm$ SD	N	M $\pm$ SD	N	M $\pm$ SD	N	M $\pm$ SD	N	M $\pm$ SD	N
<b>Duration (d)</b>										
12°C	22.8 $\pm$ 2.24	70	—	—	—	—	—	—	—	—
15°C	11.8 $\pm$ 1.60	129	30.2 $\pm$ 4.62	13	10.8 $\pm$ 1.47	24	48.9 $\pm$ 5.56	15	—	—
20°C	5.9 $\pm$ 0.73	214	17.8 $\pm$ 2.92	60	6.1 $\pm$ 0.51	63	29.1 $\pm$ 2.59	59	16.9 $\pm$ 6.57	45
25°C	3.7 $\pm$ 0.58	458	12.5 $\pm$ 2.26	52	3.6 $\pm$ 0.55	38	20.1 $\pm$ 2.66	49	12.8 $\pm$ 5.45	33
30°C	2.8 $\pm$ 0.52	147	11.3 $\pm$ 1.64	27	2.4 $\pm$ 0.50	33	17.3 $\pm$ 1.98	41	11.2 $\pm$ 2.50	29
33°C	2.7 $\pm$ 0.44	95	(8.5 $\pm$ 1.97)	(4)	(2.7 $\pm$ 0.35)	(3)	(13.2 $\pm$ 1.71)	(3)	—	—
<b>Rates (d<sup>-1</sup>)</b>										
12°C	0.044 $\pm$ 0.004	—	—	—	—	—	—	—	—	—
15°C	0.086 $\pm$ 0.010	—	0.034 $\pm$ 0.005	—	0.094 $\pm$ 0.013	—	0.021 $\pm$ 0.0025	—	—	—
20°C	0.173 $\pm$ 0.022	—	0.057 $\pm$ 0.009	—	0.165 $\pm$ 0.014	—	0.035 $\pm$ 0.0031	—	0.070 $\pm$ 0.033	—
25°C	0.280 $\pm$ 0.046	—	0.083 $\pm$ 0.014	—	0.285 $\pm$ 0.054	—	0.051 $\pm$ 0.0063	—	0.091 $\pm$ 0.036	—
30°C	0.376 $\pm$ 0.079	—	0.090 $\pm$ 0.014	—	0.429 $\pm$ 0.084	—	0.059 $\pm$ 0.0066	—	0.094 $\pm$ 0.023	—
33°C	0.376 $\pm$ 0.064	—	(0.122 $\pm$ 0.320)	—	(0.379 $\pm$ 0.051)	—	(0.077 $\pm$ 0.0098)	—	—	—

(M = mean, SD = standard deviation, N = sample size).

**Fig. 2.** Proportional duration of embryonic (E), larval (L) and pupal (P) development of *I. typographus* relative to total preimaginal developmental time (means and SD)**Fig. 4.** Developmental rates of *I. typographus* instars: experimental data (circles, means and SD), linear regressions (solid lines) based on  $15^{\circ}\text{C} \leq T \leq 25^{\circ}\text{C}$ , and nonlinear model for entire temperature range (dotted lines)**Fig. 3.** Stage-specific heat sums (degree-days, dd) of *I. typographus* based on the developmental thresholds of the linear model

strong linear relationship between temperature and development (more precisely: developmental rate, cf. BENTZ et al., 1991; KRAMER et al., 1991). Since maturation feeding was regressed to only two temperature regimes these parameters are not dependable.

The intersection of the regression line on the x-axis (i.e. rate = 0) yielded the lower developmental threshold  $DT_{LR}$  (fig. 4). The different stages turned out to have unequal  $DT_{LR}$  (table 3). The  $DT_{LR}$  of the immobile stages, i.e. eggs and pupae, exceeded that of the larval instar by roughly two centigrades.  $DT_{LR}$  of the total preimaginal development was close to the one of the larvae, biased by the predominant larval instar (cf. fig. 2).

**Table 2.** Parameters of linear regression between temperature and developmental rates of *I. typographus* instars, based on three temperature regimes (15, 20, 25°C; maturation feeding: 20, 25°C)

Instar	N	Slope	SE of slope	Intercept	SE of intercept	R <sup>2</sup>	s <sup>2</sup>
Eggs	801	1.93E-2	2.39E-4	-2.06E-1	4.73E-3	0.89	8.21E-4
Larvae	125	4.89E-3	2.74E-4	-4.00E-2	5.69E-3	0.72	1.10E-4
Pupae	125	1.73E-2	6.49E-4	-1.72E-1	1.20E-2	0.85	5.70E-4
Egg-Pupa	123	2.99E-3	1.06E-4	-2.47E-2	1.35E-4	0.87	1.70E-5
(Matur. Feeding)	78	4.19E-3	1.60E-3	-1.35E-2	3.49E-2	0.074	8.88E-2

N = sample size; SE = standard error; R<sup>2</sup> = adjusted squared multiple correlation coefficient; s<sup>2</sup> = residual mean squares.

**Table 3.** Linear regression based developmental thresholds (DT<sub>LR</sub>), average heat sums (K [degree-days, dd]) and corresponding standard errors (SE) of the preimaginal development and maturation feeding of *I. typographus*. Threshold temperatures followed by an asterisk differ significantly from that of the total preimaginal development (egg-pupa) (*t*-test,  $\alpha = 0.05$ )

Instar	DT <sub>LR</sub> (°C)	SE of DT <sub>LR</sub> (°C)	K (dd)	SE of K (dd)
Eggs	10.6*	0.15	51.8	0.64
Larvae	8.2	0.77	204.4	11.46
Pupae	9.9*	0.42	57.7	2.16
Egg-Pupa	8.3	0.48	334.2	11.83
(Maturation Feeding)	3.2	10.81	238.5	91.05

The average physiological time K (eqn. 3) required for completion of the development was longer for pupae than for eggs, though generally shorter in chronological time (cf. table 1). Due to the lower DT<sub>LR</sub>, pupae accumulate more degree-days each day and therefore need less time to reach the required heat sum. The linearity of development speed in the temperature range between 15° and 25°C is also evidenced by fig. 3. As expected the thermal sums, based on the stage-specific DT<sub>LR</sub>, remained constant in this range. For the immobile stages the linearity was even extended to higher temperatures. The general pattern outside the linear range is lower heat sums at colder temperatures and higher values at elevated temperatures. The curves for maturation feeding give only rough estimates for the reasons mentioned above.

For simulating bark beetle development under field conditions it is convenient to have an equation which is valid for all naturally occurring temperatures. The Logan/Lactin-functions fitted for this purpose (eqn. 6) are depicted in fig. 4. They represent the observed data very well as can be seen by the correlation coefficients in table 4. This table lists the fitted parameters  $\alpha$ ,  $\beta$ , and  $\gamma$ . T<sub>max</sub> as the fourth parameter, representing maximum tolerable temperature, was fitted only for the egg stage. In order to find the best model fit for the other stages, different fixed values of T<sub>max</sub> were used to estimate model parameters. The best fit was chosen by comparing F-ratio, corrected R<sup>2</sup> and parameter estimates. According to the Logan/Lactin model the developmental rate  $r$  equals  $\gamma$  at temperature T<sub>max</sub>. Thus T<sub>max</sub> does not

correspond to the upper threshold temperature (DT<sub>u</sub>). Neither the upper nor the lower developmental thresholds can be determined algebraically from eqn. 6 (LACTIN et al., 1995). By calculating the rates for a number of temperatures in the vicinity of the probable thresholds the true values could be interpolated with sufficient accuracy. The upper threshold (DT<sub>u</sub>) was in the order of 39°C, the lower (DT<sub>l</sub>) between 1.6° and 7.9°C (cf. Discussion). Additional experiments on entire bolts at 5° and 40°C proved that there is no development at these temperatures. However, at 10°C slow development did occur. The relationship between the non-linear thresholds and those of the linear regression are discussed below. The optimum temperatures (T<sub>o</sub>) (eqn. 7) were on average slightly above 30°C, that of the immobile stages being about 3 centigrades higher.

## 4 Discussion

### 4.1 Stage duration and developmental thresholds

The sandwich method allowing easy visual evaluation of the breeding and developmental process is not suited for long lasting developmental times at low temperatures because the phloem eventually becomes too dry. One has to be aware that, innate in this methodology, the duration of all instars is slightly overestimated because the transit from one stage to the next can be recorded at the earliest at the time of the next check.

The duration of the different stages compares fairly well to the data provided by ANNILA (1969). In contrast to the findings of COELN et al. (1996) the duration of all our stages showed distinct differences between the 20° and 25°C regimes. Although we could not obtain data on maturation feeding at temperatures below 20°C such activity does occur even at 10°C (ANNILA, 1969). The percentage of the maturation period relative to development up to maturity (38%) corresponds to data in the literature (WILD, 1953: one third).

The larval stage differed in some respects from the immobile stages (egg, pupa): larval development made up 60% of the total developmental time, the percentage increasing with temperature. The egg and pupal stages seem to be more adapted to higher temperatures. They possess higher developmental thresholds (DT) and, according to the Logan/Lactin model, higher optimum temperatures than larvae. Differences between stage thresholds are useful for synchronizing the stages

**Table 4.** Parameter estimates ( $\alpha, \beta, \gamma, T_{max}$ ) of the nonlinear model (LACTIN *et al.*, 1995) for the developmental rates of *I. typographus* instars ( $R^2 =$  adjusted squared multiple correlation coefficient), and resulting values [ $^{\circ}C$ ] for the lower developmental threshold ( $DT_L$ ), optimum temperature ( $T_o$ ), and upper developmental threshold ( $DT_U$ )

Instar	$\alpha$	$\beta$	$T_{max}$	$\gamma$	$R^2$	$DT_L$	$T_o$	$DT_U$
Eggs	0.12254	8.08243	40.1	-0.09805	0.97	7.9	32.0	39.4
Larvae	0.07919	12.40338	42.0*	-0.09250	0.97	8.7	29.5	39.1
Pupae	0.14977	16.65546	40.0*	-0.02341	0.97	1.6	33.3	39.9
Egg-Pupa	0.10377	9.60332	40.0*	-0.02245	0.99	5.8	30.4	38.9

\* fixed values

(BENTZ *et al.*, 1991): at cool conditions the development of pupae is slowed down while late-hatched larvae, having a lower DT than pupae, are able to catch up with already pupated individuals. This synchronization effect favors a coincident emergence of the adult beetles, which makes it easier for them to overcome the defence mechanisms of the trees. Conversely, the high DT of eggs prevents too early hatching in spring when low temperatures might be detrimental to the young larvae.

#### 4.2 Linear and nonlinear models, physiological time

Linear regression and the Logan/Lactin model are two different approaches to describe the developmental rates (WORNER, 1992). Especially at low temperatures discrepancies exist between linear and nonlinear models (e.g. CAMPBELL *et al.*, 1974; LAMB, 1992). The data showed that within the range of 15 $^{\circ}$  to 25 $^{\circ}$ C the temperature dependency of the rates was adequately represented by a straight line. Its advantages are simplicity, reasonable developmental thresholds (DT), and easy applicability in pest management. However, it slightly overestimates the DTs compared to the "real" ones. The Logan/Lactin model describes the observed data very well over the whole range of experimental temperatures. The advantages of this model are good estimations of optimum and threshold temperatures and the coverage of the entire temperature range. In some cases there were considerable differences in the lower DTs between the two approaches (tables 3 and 4). For eggs and total development the Logan/Lactin based DTs were 2.5 centigrades lower. After visual comparison with the observed data (fig. 4) these values seem reasonable. This is supported by the (slow) development observed at 10 $^{\circ}$ C with the bolt method. The DT value of 1.6 for pupae in the Logan/Lactin model differs by 8.3 centigrades and is most probably an artefact of the model.

For comparison with the few literature data on heat sums of *I. typographus* the linear model is more appropriate. ANNILA (1969) assumed a DT of 5 $^{\circ}$ C for eggs and pupae, based on direct observations at low temperatures. This is considerably lower than our calculations. Taking ANNILA's data on the immobile stages in the linear range and calculating rather than assuming the resulting DTs we end up with values around 10 $^{\circ}$ C which is similar to our findings. The somewhat confusing description of ANNILA's methodology prevents from further comparisons. ABGRALL and JUVY (1993),

using ANNILA's DT of 5 $^{\circ}$ C, reported a sum of 550 dd for the period from flight of the parents to the first teneral beetles. If we recalculate their heat sum with our average DT of 8.3 $^{\circ}$ C we obtain 365 dd which is only slightly above our sum. The preimaginal DT of 11.8 $^{\circ}$ C reported by COELN *et al.* (1996) appears to be exceptionally high.

The results of the present study base on constant temperatures. Though fluctuating temperatures as they are occurring in the field are reported to have deviating effects on development particularly at the extremes (BEHRENS *et al.*, 1983; WORNER, 1992), our stage-specific data should provide a basis on the one hand to evaluate the current or potential development of a population in the field at given climatic conditions (pest management) and on the other hand to parametrize simulation models of this bark beetle species.

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#### References

- ABGRALL, J. F.; JUVY, B., 1993: Incidence de la température sur le développement du Typographe, *Ips typographus* L. (Coleoptère, Scolytidae) en zones montagneuses. Inform. Techn. CEMAGREF **90**, 1-7.
- ANNILA, E., 1969: Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). Ann. Zool. Fenn. **6**, 161-208.
- BALOGUN, R. A., 1969: A perspex-bark sandwich technique for rearing bark beetles. Bull. Entomol. Soc. Nigeria **2**, 85-86.
- BEHRENS, W.; HOFFMANN, K. H.; KEMPA, S.; GÄSSLER, S.; MERKEL-WALLNER, G., 1983: Effects of diurnal thermoperiods and quickly oscillating temperatures on the development and reproduction of crickets, *Gryllus bimaculatus*. Oecologia **59**, 279-287.
- BENTZ, B. J.; LOGAN, J. A.; AMMAN, G. D., 1991: Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. Can. Entomol. **123**, 1083-1094.
- CAMPBELL, A.; FRASER, B. D.; GILBERT, N.; GUTIERREZ, A. P.; MACKAUER, M., 1974: Temperature requirements of

- some aphids and their parasites. *J. Appl. Ecol.* **11**, 431–438.
- COELN, M.; NIU, Y.; FÜHRER, E., 1996: Entwicklung von Fichtenborkenkäfern in Abhängigkeit von thermischen Bedingungen verschiedener montaner Waldstufen. *Entomol. Gener.* **21**, 37–54.
- DRAPER, N. R.; SMITH, H., 1981: Applied regression analysis. New York: John Wiley & Sons.
- FÜHRER, E., 1981: Jahreszeitliche Qualitätsschwankungen des Fichtenbastes (*Picea excelsa* Link) als Brutsubstrat für den Borkenkäfer *Pityogenes chalcographus* L. (Col., Scolytidae). *Z. Ang. Entomol.* **91**, 74–83.
- HOPPING, G. R., 1961: Techniques for rearing *Ips* De Geer (Coleoptera: Scolytidae). *Can. Entomol.* **93**, 1050–1053.
- KINN, D. N.; MILLER, M. C., 1981: A phloem sandwich unit for observing bark beetles, associated predators, and parasites. *U.S. For. Serv. Res. Note SO 269*, 1–3.
- KRAMER, D. A.; STINNER, R. E.; HAIN, F. P., 1991: Time versus rate in parameter estimation of nonlinear temperature-dependent development models. *Environ. Entomol.* **20**, 484–488.
- LACTIN, D. J.; HOLLIDAY, N. J.; JOHNSON, D. L.; CRAIGEN, R., 1995: Improved rate model of temperature-dependent development by arthropods. *Environ. Entomol.* **24**, 68–75.
- LAMB, R. J., 1992: Developmental rate of *Acyrtosiphon pisum* (Homoptera: Aphididae) at low temperatures: implications for estimating rate parameters for insects. *Environ. Entomol.* **21**, 10–19.
- LOBINGER, G., 1994: Die Lufttemperatur als limitierender Faktor für die Schwärmaktivität zweier rindenbrütender Fichtenborkenkäferarten, *Ips typographus* L. und *Pityogenes chalcographus* L. (Col., Scolytidae). *Anz. Schädl.kd. Pflanzenschutz Umweltschutz* **67**, 14–17.
- LOGAN, J. A.; WOLLKIND, D. J.; HOYT, S. C.; TANIGOSHI, L. K., 1976: An analytical model for description of temperature dependent rate phenomena in arthropods. *Environ. Entomol.* **5**, 1133–1140.
- MERKER, E., 1951: Das Wetter der Jahre 1939 bis 1950 und sein Einfluss auf die Massenvermehrung des grossen Fichtenborkenkäfers in Südbaden I,II. *Allg. Forst- Jagdztg.* **123**, 213–233.
- SCHLYTER, F.; CEDERHOLM, I., 1981: Separation of the sexes of living spruce bark beetles, *Ips typographus* (L.), (Coleoptera: Scolytidae). *J. Appl. Entomol.* **92**, 42–47.
- VITÉ, J. P., 1952: Temperaturversuche an *Ips typographus* L. *Zool. Anz.* **149**, 195–206.
- WILD, M., 1953: Die Entwicklung des grossen Fichtenborkenkäfers *Ips typographus* L. im Hochschwarzwald (1000–1200 m ü.M.) und ihre Abhängigkeit vom Klima 1947–1950. *Ber. Nat.forsch. Ges. Freiburg* **43**, 121–176.
- WORNER, S. P., 1992: Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. *Environ. Entomol.* **21**, 689–699.
- WULF, A.; KEHR, R., 1991: Borkenkäfer-Gefahren nach Sturmschäden: Möglichkeiten und Grenzen einer integrierten Bekämpfung. *Mitt. Biol. Bundesanst. Land-Forstw., Berl.-Dahl.* **267**, 1–227.

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