Eur. J. Entomol. **111**(2): 207–215, 2014
doi: 10.14411/eje.2014.030
ISSN 1210-5759 (print), 1802-8829 (online)

Does the prediction of the time of egg hatch of *Thaumetopoea processionea* (Lepidoptera: Notodontidae) using a frost day/temperature sum model provide evidence of an increasing temporal mismatch between the time of egg hatch and that of budburst of *Quercus robur* due to recent global warming?

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Key words. Lepidoptera, Notodontidae, *Thaumetopoea processionea*, oak processionary moth, temperature sum, phenology, synchrony, oak foliation, climate change

Abstract. *Thaumetopoea processionea* is a serious defoliator of oak and of medical concern whose abundance has consistently increased throughout Europe during the past two decades. This study validates a previously published frost day/temperature sum model for predicting time of egg hatch of this species using five years of recent field data from South-West Germany. This model proved satisfactory for predicting the time of egg hatch of *T. processionea*. Hence, the model was used to retrospectively predict the time of egg hatch of *T. processionea* in the Karlsruhe area, which indicates that the time of egg hatch has fluctuated over the past 130 years. In the last two decades, however, predicted time of egg hatch is much earlier than the long-term average due to the increase in winter and early spring temperatures. Comparison of predicted time of egg hatch of *T. processionea* and long-term records of the time of foliation of its common host *Quercus robur* revealed that in the study area the temporal advance in the timing of both events was similar. This is not in accordance with recently published research on spring-feeding folivores, which report a diverging trend in the timing of egg hatch and budburst of their host plants as a consequence of human-induced climate change.

INTRODUCTION

The prediction of the onset of active development of insect pests has long been used in applied forest, agricultural and horticultural research. Prediction of egg hatch is particularly important in determining the most effective time to apply control measures. Moreover, forecasting the effects of climate change on insect population dynamics relies on precise phenological modelling. Since physiological processes are temperature-dependent, insect development is generally faster at high than low temperatures. Most models used to predict insect development, therefore, include temperature as the main parameter (e.g. Bentz et al., 1991; Lactin et al., 1995; Logan et al., 2006; Baier et al., 2007; Jalali et al., 2010). An increasing number of studies have attributed accelerated development to global warming (Robinet & Roques, 2010; Stange & Ayres, 2010). Further consequences of climate change are range expansions (Battisti et al., 2005), an increase in the number of broods in multivoltine species (Yamamura & Kiritani, 1998; Lange et al., 2006) or temporal disruption of herbivore/host, plant/pollinator and predator/prey systems (Visser et al., 1998; Visser & Holleman, 2001; Hegland et al., 2009; Donnelly et al., 2011), the latter presumably affecting specific population dynamics and pest potential (Williams & Liebhold, 2002; Donnelly et al., 2011).

The western Palaearctic genus *Thaumetopoea* Hübner includes over a dozen species of notodontid moths whose social caterpillars feed on deciduous tree leaves or coniferous needles and release minute irritant setae when disturbed (Simonato et al., 2013). These setae can have lasting effects on human and animal health (Maier et al., 2004; Gottschling & Meyer, 2006, Jans & Franssen, 2008). As defoliators, they may adversely affect carbon sequestration and even the vitality of the host trees, causing losses in forest productivity (Jacquet et al., 2013), severe damage to forest stands (e.g. Delb et al., 2008; Nageleisen, 2013) and economic losses in forestry (Kriticos et al., 2013). The study species, *Thaumetopoea processionea* Linné (oak processionary moth), is widely distributed throughout Europe and parts of the Middle East (Groenen, 2010; Groenen & Meurisse, 2012). Since the 1990s, outbreaks of *T. processionea* have increasingly been reported in many European countries (Roskams, 1995; Stigter & Romeijn, 1992; Bogenschütz, 1998; Roversi, 2008; Wagenhoff & Delb, 2011). Increases in population densities are mostly attributed to global warming (e.g. Moraal & Jagers op Akkerhuis, 2011), but the causal relationship is not yet fully understood (Klapwijk et al., 2013). Females of univoltine *T. processionea* lay their egg batches on the shoots of oak trees in late summer. Embryonic development is completed by early autumn when neonates enter diapause and hibernate in their eggs until early spring the following year. Larval eclosion occurs within a few days and generally precedes oak foliation (Meurisse et al., 2012; Wagenhoff & Veit, 2011; Wagenhoff et al., 2013). Visser & Holleman

(2001) developed a frost day/temperature sum model for the prediction of winter moth (*Operophtera brumata* Linné) egg hatch which was first adopted for *T. processionea* by Custers (2003). This model predicts that the thermal requirements for egg hatch decrease with increase in the occurrence of preceding frost events. To test this hypothesis, we collected field data on time of egg hatch of *T. processionea* and compared it with temperature records from nearby weather stations. In addition, we conducted a laboratory experiment in which sibling neonates were exposed to two different numbers of frost events. In order to assess whether global warming is a likely cause of increased population densities, we also used this model to estimate time of egg hatch of *T. processionea* retrospectively for the Karlsruhe area using a long-term data set of historic temperature records. As temporal synchrony of egg hatch and host budburst is thought to be an important factor in population dynamics in spring-feeding folivores (e.g. Varley & Gradwell, 1968), we compared the hatching phenology of *T. processionea* with the time of budburst of its common host *Quercus robur* Linné. Accordingly, the aim of this study was (1) to validate a model for predicting time of egg hatch in the spring-feeding oak defoliator and medical pest *T. processionea* and (2) to investigate if there is a temporal shift in the timing of egg hatch of *T. processionea* due to global warming, possibly resulting in a mismatch or even better match with oak foliation phenology.

MATERIAL AND METHODS

Field study sites

Thaumetopoea processionea egg hatch was observed at two study sites in South-West Germany. Site 1 is located near the city of Freiburg i. Br. (47°59´N, 7°47´E; 233 m a.s.l.). The trees (*Quercus robur*) are planted in rows in an open landscape. The local *T. processionea* population was detected for the first time during a mass outbreak and extensive defoliation in 2007. Site 2 is a 20 ha mixed stand of 64–179 year old oaks [*Q. robur* and *Q. petraea* (Mattuschka) Lieblein] located near Brackenheim-Duerrenzimmern (49°05´N, 9°05´E; 220 m a.s.l.). From 2006–2011, a local outbreak was observed which resulted on several occasions in extensive defoliation and occasional die-back of single oak trees. In 2012, the moth population suddenly collapsed and since then it has remained at a low level.

Observation and prediction of egg hatch

In order to determine the time of egg hatch of *T. processionea* during 2009–2013, egg batches were marked at both study sites and surveyed daily from late March/early April until egg hatch. The egg batches were on twigs at a height of approx. 1–4 m. As the time of egg hatch did not depend on cardinal direction (unpublished data) the side of the twigs on which the eggs were laid was not taken into account. Each day, the number of egg batches that had hatched was recorded at site 1 in 2009 (a total of 42 egg batches on 9 oak trees), 2010 (84/16), 2011 (132/15), 2012 (86/15) and 2013 (13/8), and at site 2 in 2012 (58/7) and 2013 (11/3). Furthermore, a transfer experiment was conducted, whereby egg batches were transferred between the two study sites as well as being stored for different lengths of time at the research facility. Consequently, several egg batches were exposed to one of ten different temperature regimes (temperature sum and frost days), thereby increasing the spread of values for a more informative regression line. The results for several egg batches that developed under the same temperature regime were pooled and treated as one sample and are represented by a single data point in the regression line. On 27 January 2011, 79 egg batches from four oak trees at site 2 were transferred to the Forest Research Institute of Baden-Wuerttemberg (FVA) in Freiburg (47°58´N, 7°50´E; 298 m a.s.l.) and exposed outside the institute building. One month later, 63 of these egg batches were transferred to site 1 and 16 egg batches were left outside the institute. Finally, 17 egg batches from site 1 were directly transferred to site 2 on 1 February 2013. Twigs carrying egg batches were cut and directly transferred in Petri dishes to the new site where they were wired onto branches beside other marked batches at a height of approx. 1–4 m. In total the hatching dates of ten samples of egg batches were collected. Each year from 2009–2013, roughly the same amount of time was spent searching for egg batches. Hence, the number of marked egg batches per year ranged between 11 and 132 and is assumed to be a representative percentage of the population, respectively. For modelling, the variable "egg hatch" was defined as the median Julian date, i.e. when at least 50% of the egg batches in each sample started to hatch. All of these sites were at least within 6 km of a weather station and were situated within the same climatic region as the corresponding weather station. Daily minimum and maximum temperatures were obtained from the weather stations "Brackenheim" (49°08´N, 9°06´E; 229 m a.s.l.) and "Mengen" (47°96´N, 7°70´E; 211 m a.s.l.) run by the Landwirtschaftliches Technologie Zentrum Augustenberg (LTZ) and the weather station "Freiburg" (48°00´N, 7°85´E; 300 m a.s.l.) run by the Deutscher Wetterdienst (DWD). The weather station "Mengen" was closest to site 1, "Brackenheim" to site 2, and "Freiburg" to the FVA institute.

The phenological frost day/temperature sum model published by Visser & Holleman (2001) predicts a negative linear relationship between the number of frost days (days with an absolute minimum temperature below 0°C) and the required temperature sum until the date of egg hatch. For this study, we adjusted the model to the biology of *T. processionea*, which lays its eggs from mid-July to early September. Hence, the number of frost days was summed from 1 September and the corresponding thermal requirement from the winter solstice (21 December) until the date of median egg hatch. The selection of winter solstice is considered to be appropriate as in other insects (e.g. *Pyrrhocoris apterus* L.) winter diapause is completed around that date (Hodkova & Hodek, 2004). The thermal requirement for each sample was calculated by accumulating daily temperature sum using a single sine-wave function with a lower horizontal cut-off at +2.6°C (Custers, 2003). Calculations were computed with a freeware programme provided by the University of California (http://www.ipm.ucdavis.edu/WEATHER/index.html). Data collected from 2009–2012 (four seasons) was used for *model building* and the 2013 data for *model validation*.

Laboratory study of the time of egg hatch of *T. processionea*

Twenty-five egg batches were collected at site 1 on 2 December 2011 and stored outside the FVA building. On 2 January 2012, after experiencing a total of 28 frost days, the egg batches were transferred to a refrigerator (Liebherr KGK 3955) and kept in the dark at a relative air humidity of 58% and a mean temperature of +1.6°C, which is below the lower thermal threshold of +2.6°C for *T. processionea* egg hatch (Custers, 2003). Daily minimum temperatures (records taken every half an hour) frequently fell below 0°C, simulating additional frost events. After a total of 44 frost days, each of the egg batches was split in two. One half was transferred to a climate chamber (Ehret KBK 4330; at a constant temperature of +13°C, 11.5L : 12.5D) whereas the second half was left in the refrigerator for another 15 frost days. After a total of 59

Table 1. Yearly dates of the median time of egg hatch of *Thaumetopoea processionea* and the corresponding hatching period [days], number of frost days, temperature sum [degree-days] and deviation [days] between observed and predicted time of egg hatch (using a modified model of Visser & Holleman, 2001) (origin and sites at which the egg batches were observed; n – number of egg batches observed; white area – data used to determine the parameters; greyish area – data used to validate the model). The weather stations assigned to the different study sites were: Study site 1: "Mengen" (LTZ); study site 2: "Brackenheim" (LTZ); FVA institute: "Freiburg" (DWD).

Year	Origin site	Observation site	n	Period	Egg hatch (real)	Egg hatch (model)	Deviation	Frost days	Temperature sum
2009	study site 1	study site 1	42	≤ 7	6 April	7 April	+1	109	208.9
2010	study site 1	study site 1	84	10	7 April	6 April	–1	95	275.1
2011	study site 1	study site 1	132	8	29 March	29 March	0	92	271.4
2011	study site 2	study site 1	63	5	31 March	1 April	+1	78	305.0
2011	study site 2	FVA institute	16	8	1 April	1 April	0	74	335.0
2012	study site 1	study site 1	86	8	30 March	3 April	+4	70	318.4
2012	study site 2	study site 2	58	17	12 April	10 April	–2	58	399.5
2013	study site 1	study site 1	13	2	17 April	16 April	–1	79	331.3
2013	study site 1	study site 2	17	3	17 April	17 April	0	84	310.9
2013	study site 2	study site 2	11	2	18 April	18 April	0	82	312.7

frost days, the second half of each egg batch was also transferred to the same climate chamber. Egg hatch was monitored using a digital web camera (Logitech®, HD Pro Webcam C920) to avoid disturbing the eggs. The temperature sum expressed as degree-days (lower threshold: +2.6°C) was calculated for the date of egg hatch and compared with the number of frost days experienced.

Estimating the time of egg hatch of *T. processionea* in the Karlsruhe area over the period 1877–2011

The area of Karlsruhe was selected for two reasons. Firstly, it is located within the Upper Rhine valley, which is one of the hot spots of *T. processionea* infestations in South-West Germany. Secondly, there is daily temperature data (1876–2011) for this region. Daily minimum and maximum temperatures from 1876–2008 were provided by the DWD (weather station "Karlsruhe": 49°02´N, 8°21´E; 112 m a.s.l.). Data recording at this weather station ceased in 2008 and thus temperature measurements were obtained from the 7.5 km distant DWD weather station "Rheinstetten" (48°97´N, 8°31´E; 109 m a.s.l.). Missing daily temperature values for the 2009–2011 period in Karlsruhe were interpolated using a linear regression derived from 38 years of daily average temperature values (n = 13,696) recorded at both weather stations ($R^2 = 0.991$; equation: $T_{Karlsruhe}$ [°C] = $0.996 * T_{Rheinstetten} + 0.4023$). The date of egg hatch was retrospectively predicted for each year from 1877 to 2011, except for 1945–1947 (due to missing data), using the frost day/temperature sum model adapted for *T. processionea*. Using the estimated annual egg hatch data, mean egg hatch was calculated for each decade (1880–1889, […], 2000–2009) and the deviations of the decadal means from the overall mean (1877–2011) were calculated. In order to check if delayed (or advanced) egg hatch was based on fewer (or a higher number of) frost days or rather lower (or higher) winter and spring temperatures, the same approach was applied to the number of frost days from 1 September onwards and the temperature sums (lower threshold: +2.6°C) from 21 December onwards to a fixed date (1 April), respectively.

T. processionea egg hatch in relation to *Q. robur* foliation (1961–2011)

A continuous yearly data set on *Q. robur* foliation (i.e., when leaf size reached the size of a mouse ear) was available for the period 1961 to 2011 (with the exception of 1962, 1963, 1967 and 1970) from the DWD phenological station "Wiesental" (49°13´N, 8°31´E; 110 m a.s.l.), 25 km northeast of the city of Karlsruhe and within the corresponding climatic region of egg hatch prediction. In order to test for a potential temporal mismatch of egg hatch and oak foliation (expressed as the number of days between these two events) due to global warming, the means of the following two time periods were compared: 1961–1992 and 1993–2011. These time periods were selected on the basis of the statistical breakpoint in the relationship of the date of oak foliation across years, which occurred in 1993 (see Results). Finally, Meurisse et al. (2012) have shown that the ability of neonate larvae to survive starvation prior to budburst strongly decreases with increasing temperatures. Hence, the temperature sum (base temperature: 0°C) of a fixed time period (12 days) following predicted egg hatch was calculated for each year in order to determine if the temperature sum in that critical time period has increased over the past 50 years. This might indicate that the risk of neonate mortality has increased under global warming due to a temporal mismatch, i.e., period of neonate starvation exceeds one and a half weeks. A 12-day period was selected in order to take into account the average preceding egg hatch versus oak foliation (see Results).

Statistical analysis

All analyses were run in statistical programme R and statistical significance determined at a α = 0.05 level. The frost day/temperature sum model of *T. processionea* egg hatch was validated using simple linear regression analysis. Predicted egg hatch and observed oak foliation for the period 1961–2011 were analyzed using piecewise linear regression analysis with R package "segmented" (Vito & Muggeo, 2008). Progress of temporal mismatch between oak foliation and egg hatch, as well as that of the 12-day temperature sum following predicted egg hatch from 1961–2011 were analyzed using correlation analysis. In addition, comparison of temporal mismatch of oak foliation and egg hatch for the periods 1961–1992 and 1993–2011 was performed using Student's t-test. Egg hatch after 44 or 59 frost days in the laboratory were compared using a paired t-test.

RESULTS

Predicted and observed time of egg hatch of *T. processionea*

Egg hatch of *T. processionea* in the field occurred in the 4th week of March or first three weeks of April (Table 1).

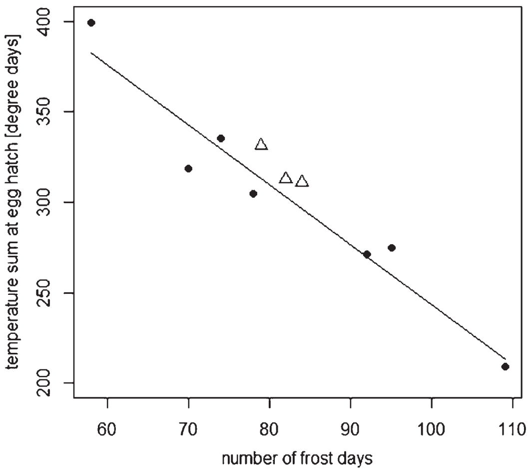

Fig. 1. Relationship between the temperature sum at the median time of the egg hatch of *Thaumetopoea processionea* and the number of frost days recorded at both study sites between 2009 and 2012 (black spots: data used to develop the model) and in 2013 (triangles: data used to validate the model).

Neonate hatching in the samples of batches surveyed took on average 7 days (range: 2–17 days; Table 1). In accordance with the findings of Visser & Holleman (2001), the required temperature sum for egg hatch significantly decreased linearly with increase in the number of frost events during 2009–2012 ($n = 7$; adjusted $R^2 = 0.93$; $p = 0.0003$; Fig. 1). The predictive model for the temperature requirement for egg hatch based on records of daily minimum and maximum temperatures from 2009–2012 for the study sites is as follows:

$$TS = -3.327 * FD + 575.66 \qquad [1]$$

where TS is the temperature sum (21 December until median egg hatch), and FD the number of frost days (1 September until median egg hatch). Discrepancies between the observed and predicted times of egg hatch ranged between –2 to +4 days (Table 1). Validation of the model using 2013 data proved satisfactory as in two cases the observed and predicted times of egg hatch coincided and in one case there was a discrepancy of 1 day between the two (Table 1; Fig. 1).

Laboratory study of egg hatch

Increasing the number of preceding frost days significantly reduced the thermal requirements for egg hatch (paired t-test: $t = 11.664$; $df = 24$; $p < 0.0001$). The temperature sums in the 44 and 59 frost day treatments were 232.3 ± 15.5 (mean ± SD) and 201.3 ± 15.3 degree-days, respectively.

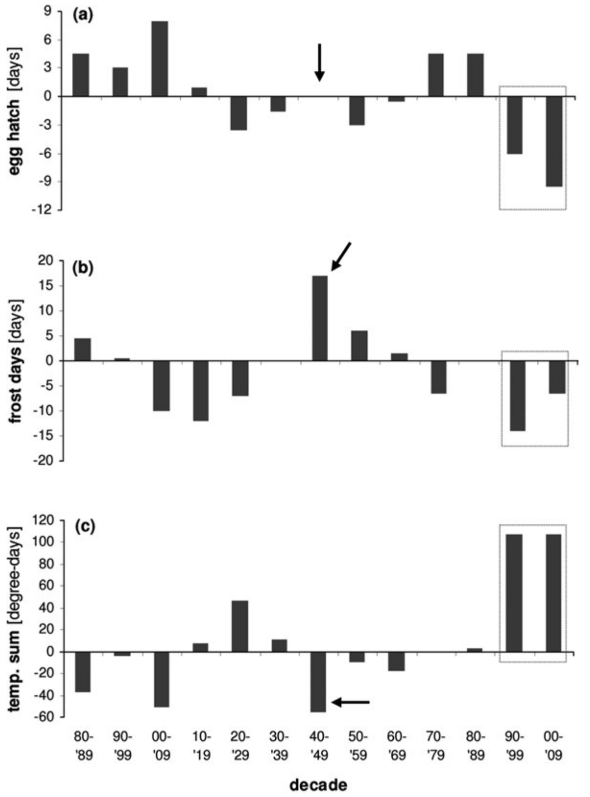

Fig. 2. Deviations of the decadal means of (a) the predicted times of egg hatch of *Thaumetopoea processionea*, (b) the number of frost days (1 September – 1 April) and (c) the temperature sum (21 December – 1 April) from the corresponding overall 130 year averages (black arrows and dotted rectangles see text).

Estimating the time of egg hatch of *T. processionea* in Karlsruhe from 1877–2011

The estimated average Julian date for the egg hatch of *T. processionea* in the vicinity of Karlsruhe over the period 1877–2011 based on the frost day/temperature sum model (equation [1]) is 106 (range: 80–127), corresponding to 16 April (range: 21 March – 7 May). Accordingly, egg hatch was delayed compared to the overall average (1877–2011) in the decades in the periods 1880–1919 and 1970–1989, respectively. In contrast, egg hatch preceded the long-term average date in decades in the 1920–1939 and 1950–1969 periods, and strikingly so during the past two decades (1990–2009) (Fig. 2a). For the 1940–1949 decade, predicted time of egg hatch was close to the average hatching period (see arrows in Fig. 2a). In this period, increased incidence of winter frosts (Fig. 2b) compensated for the lower spring and winter temperatures (Fig. 2c). Within the

Table 2. The results of the regression analysis of the chronological sequence of (1) time of egg hatch of *Thaumetopoea processionea* and (2) foliation of *Quercus robur* in the study area "Karlsruhe" (models: simple linear regression vs. piecewise linear regression; see also Fig. 3).

	Simple linear model		Segmented linear model			
	R^2 (adjusted)	p	R^2 (adjusted)	Breakpoint (year ± SE)	p (segmented vs. linear)	p (slope)*
Egg hatch	0.1987	0.0006	0.2281	1979 ± 7.1	0.1563	0.22
Oak foliation	0.2513	0.0002	0.4334	1993 ± 3.3	0.0009	0.0005

* Davies' test.

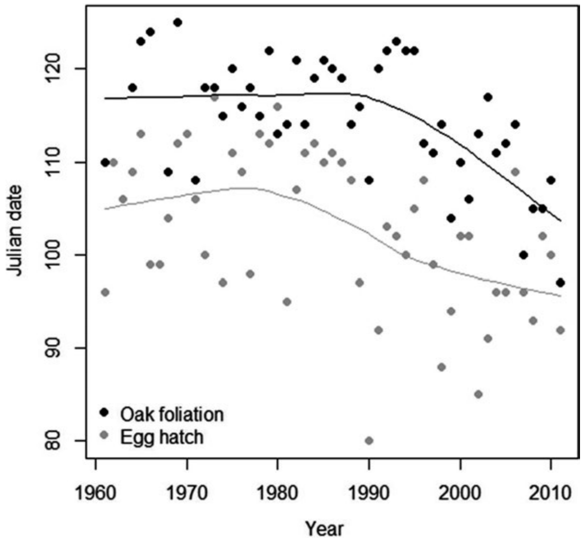

Fig. 3. Smoothed scatterplot of the yearly Julian dates of the predicted median time of egg hatch of *Thaumetopoea processionea* (grey) and recorded foliation of *Quercus robur* (black) in the Karlsruhe area from 1961–2011 (see also Table 2). Data on the foliation of *Q. robur* were obtained from the DWD phenological station "Wiesental".

1990–2009 period, the number of frost days decreased (see rectangle in Fig. 2b) while winter and spring temperatures increased (Fig. 2c); that is, higher temperatures more than compensated for a lower number of frost days resulting in accelerated egg hatch compared to the long-term decadal average (Fig. 2a).

Egg hatch in relation to *Q. robur* foliation (1961–2011)

The estimated time of egg hatch of *T. processionea* preceded recorded time of foliation of *Q. robur* by 12 days on average during the period 1961–2011. Mean decadal mismatch was 13 days (1961–1970), 8 days (1971–1980), 13 days (1981–1990), 17 days (1991–2000) and 12 days (2001–2010). Both phenological events occurred significantly earlier than in the 1960s (Table 2). However, visual inspection of the data indicates that the dates of egg hatch of *T. processionea* and foliation of *Q. robur* initially varied around a constant value, but have increasingly occurred earlier since the 1980s and the beginning of the 1990s, respectively (Fig. 3). A piecewise linear regression model was a significantly better fit to the oak foliation data than the simple linear model and identified a breakpoint in the year 1993. The most likely breakpoint for egg hatch was 1979; however the piecewise model was not a significantly better fit than the simple linear model (Table 2).

There was no difference in the mean days of mismatch for the time periods 1961–1992 and 1993–2011 (t-test: t = 0.44; df = 37.91; p = 0.66; Fig. 4). Consequently, this analysis does not support a divergence in the temporal asynchrony between these two phenological events (Pearson's r = 0.019, p = 0.69, n = 47). Assuming that the larvae do not feed on average for 12 days following median egg hatch, the corresponding temperature sum has not changed since 1961 (Pearson's coefficient = 0.008, p = 0.25, n = 46; Fig. 5), indicating that the risk of dying of starvation due to higher temperatures after egg hatch has not increased.

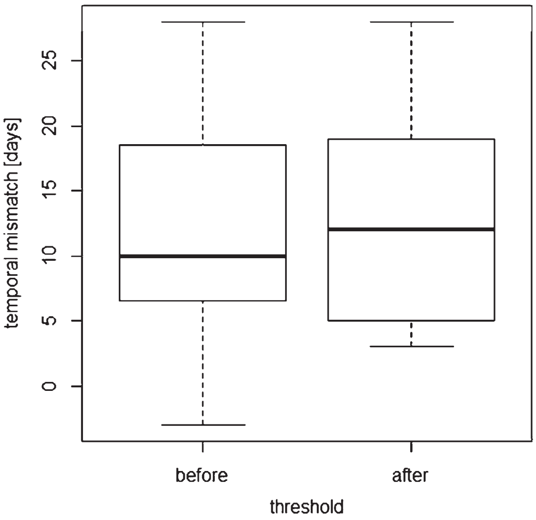

Fig. 4. Temporal mismatch in the time of egg hatch of *Thaumetopoea processionea* and budburst of *Quercus robur* in the study area between 1961–1992 and 1993–2011.

DISCUSSION AND CONCLUSIONS

Prediction of the time of egg hatch has become an essential tool for assessing the effect of climate change on the population dynamics of spring-feeding folivores such as *T. processionea*. Neonate survival and subsequent female fecundity of these species are generally best when egg hatch and budburst are synchronized (Van Asch & Visser, 2007). Larvae that hatch too early may die of starvation whereas those that hatch too late have to cope with a rapid decline in leaf quality (Feeny, 1968; Forkner et al., 2004). Based on the results of our field and laboratory study on egg hatch, we were able to corroborate the findings of Custers (2003) as the frost day/temperature sum model indicates that the thermal requirements for *T. processionea* neonate eclosion is reduced by an increase in the number of frost days. The number of days below the developmen-

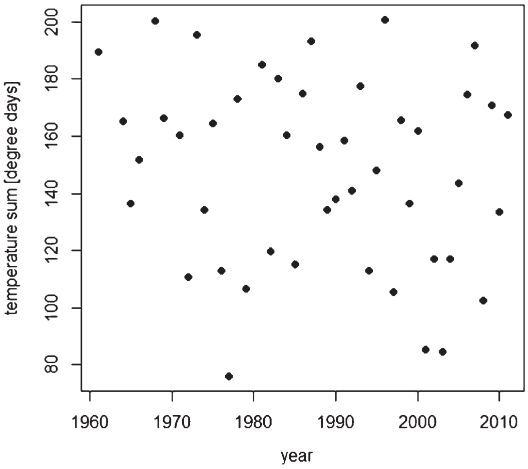

Fig. 5. Scatterplot of the yearly temperature sum (base temperature: 0°C) for the 12 day period following egg hatch of *Thaumetopoea processionea*.

tal zero or below 0°C also decreases the temperature sum necessary for egg hatch in other species, for example, the winter moth *Operophtera brumata* (Visser & Holleman, 2001; Kimberling & Miller, 1988).

A possible explanation for this phenomenon might be that the number of frost days is a suitable predictor of the progress of the harsh and inhospitable winter months ("memory of the winter": Amasino, 2004) and the length of time to the onset of the growing season. The more frost days the larvae have experienced, the higher the probability that winter is already over. Hence, this adaptation would prevent the larvae from hatching too early during warmer periods in the winter months as well as hatching too late when the growing season is already well advanced. Our data for a range of 58–109 frost days and 209–400 degree-days (Table 1) indicates that the relationship between thermal requirements and chilling is linear. However, the relationship might be non-linear when numbers of frost days and temperature sum values are greater than those included in this study. Van Ash & Visser (2007) state that linear relationships become non-linear at extreme temperatures as physiological processes slow down due to enzyme inactivation. Consequently, they assume that in the field phenological processes start later than predicted. Moreover, they hypothesized that hibernating insects use the same cues as their host plants to ensure synchronisation. Indeed, for several tree species the thermal sum necessary for budburst decreases with successive numbers of chill days (Cannell & Smith, 1983; Harrington et al., 2010). Consequently, our observations on egg hatch in *T. processionea* support the above mentioned hypothesis that herbivores use the same environmental cues as their hosts. However, it has to be emphasized that although modelling of budburst in forest trees has been the subject of many studies and quite a few models exist (for an overview see Hänninen, 1995; Hänninen & Kramer, 2007), the underlying physiological processes are not fully understood. This is also true for *T. processionea*. Even though the presented model proved satisfactory for predicting the time of egg hatch, the underlying mechanisms are unknown. Generally, winter diapause in insects of cold temperate climates is regarded as a two-phase process including (1) endogenous *diapause* followed by (2) post-diapause *quiescence* (e.g. Hodek, 2002; Raak-van den Berg et al., 2013). The first phase, *diapause*, is a state of arrested development, which is usually induced and may be terminated by environmental stimuli, mostly photoperiod (e.g. Hodkova & Hodek, 2004; Zeng et al., 2013). In the field, winter diapause is often completed in early/mid-winter (Hodek, 2002), and cool temperatures or frost may accelerate its completion (Hodek, 2002; Hodkova & Hodek, 2004). During the second phase, *quiescence*, development is linearly and directly dependent on temperature, provided ambient temperatures are within the range of the upper and lower developmental thresholds. Similar concepts are suggested for plant phenology in spring (Saxe et al., 2001). In particular, temperature and photoperiod are regarded as the two best predictors of budburst in forest trees, including *Q. robur* (Schaber & Badeck, 2003). However, the effects of photoperiod on *T. processionea* diapause and egg hatch remain to be studied. Even though winter dormancy in *T. processionea* has not been studied in detail, it appears that the neonates inside their eggs enter a state of "true" diapause, i.e. endogenous arrested development, of unknown duration. Egg batches that were collected in early September and kept indoors at room temperature failed to hatch (own unpubl. observ.) but those collected at the end of November and kept indoors at a constant 25°C hatch (Bogenschütz, 2011, pers. commun.).

The frost day/temperature sum model enabled us to retrospectively estimate the time of egg hatch of *T. processionea* in the Karlsruhe area. Analysis revealed that egg hatch generally precedes oak foliation, which accords with previous findings (Custers, 2003; Meurisse et al., 2012; Wagenhoff et al., 2013). The time of egg hatch in the study area has varied markedly over the past 130 years. There is a clear trend, however, as the time of egg hatch of *T. processionea* has increasingly occurred earlier in the year since the beginning of the 1990s. This shift can be mainly ascribed to increasing winter and early spring temperatures over the past two decades. Phenological data on foliation suggests that there is a similar trend in the time of foliation of *Q. robur*. Budburst of *Q. robur* is recorded as occurring earlier over the past few decades in other areas of Germany and in Slovenia (Menzel et al., 2008). Our results are therefore in line with other results indicating that certain phenological traits of animals and plants are occurring earlier as consequence of global warming (Walther et al., 2002; Root et al., 2003, 2005; Thackeray et al., 2010).

It is suggested that phenological shifts induced by anthropogenic climate change lead to a mismatch in the timing of the life stages in different trophic levels (Visser et al., 1998; Visser & Both, 2005). Considering that the phenological synchronisation of folivores with their hosts evolved via natural selection over a long period of time, it is likely that it will be disrupted when phenological changes in the hosts take place over a time period too short for the herbivores to adapt (Visser & Holleman, 2001; Van Asch & Visser, 2007). A mismatch increases the risk of neonates either experiencing extended periods of starvation or having to feed on poor quality foliage. A trend in the divergence between the time of egg hatch of *T. processionea* and budburst of oak of 3 days per decade, which has extended the period for which the neonates starve in early spring, has been suggested by Meurisse et al. (2012). However, data we collected in South-West Germany indicate that there has not been a diverging change in the relationship between the time of egg hatch of *T. processionea* and that of foliation of oak up to 2011. Inconsistencies in the results of these two studies may be due to regional differences or the use of different models for determining the time of egg hatch of *T. processionea*. Therefore, the assessment of future changes in the time of egg hatch of *T. processionea* relative to the budburst phenology of oak in a changing climate is still uncertain and should be treated with caution when used to consider consequences at a broader scale. Predicting future changes in population dynamics of the system is uncertain because of (1) discrepancies between the phenological models and reality, (2) uncertainty about the climatic models and (3) the fact that the potential of the folivore to adapt to changes in its host is not taken into account.

Even if synchrony is currently not disrupted, it may nevertheless be disrupted in the future as it is generally predicted that the rate of global warming is likely to increase (IPCC, 2007). However, increasing winter temperatures reduce the incidence of frost days, which in turn results in an increase in the number of degree-days required for egg hatch. On the other hand, with increased spring temperatures the thermal requirements may be achieved earlier. Consequently, a decrease in the number of frost days in winter and higher temperatures in spring may cancel each other out in terms of their effects on the time of egg hatch. The data analyzed indicates that higher winter temperatures have more than compensated for the fewer frost days recorded over the last two decades and as a result the time of egg hatch of *T. processionea* has been occurring earlier. However, this may change when global warming is more advanced. In Douglas-fir for instance, where chilling reduces the thermal requirements for budburst, the climate change induced trend towards earlier budburst is reversed when temperatures during winter rise markedly (Harrington et al., 2010). However, even if the phenological shift in herbivore hatching parallels budburst of its host, rising temperatures may be harmful as they significantly reduce the ability of the neonates to survive starvation (Wint, 1983; Hunter, 1990; Meurisse et al., 2012). For our study area and the time period analyzed, there is no evidence of increased temperatures occurring within the pre-feeding period. However, this might change if global warming were to accelerate. If this were the case, *T. processionea* is likely to be adversely affected by climate change, which contradicts the often stated assumption that *T. processionea* benefits from global warming. However, freshly hatched *T. processionea* neonates are able to survive three weeks of starvation (Meurisse et al., 2012; Wagenhoff et al., 2013), which would be sufficient for them to mostly compensate for any possible divergence in the timing of egg hatch and budburst. Furthermore, variability in the time of egg hatch and ability to survive starvation (Wagenhoff et al., 2013) may enable *T. processionea* to adapt to extended asynchrony via natural selection. In this respect, high selective pressure is thought to quickly restore temporal synchrony in spring-feeding folivores (Dixon, 2003; Van Asch et al., 2007; Robinet & Roques, 2010). Moreover, global warming presumably reduces both, the frequency of severe winter frosts and late frosts that can negatively affect the survival of pharate neonates and caterpillars due to frost injury or destruction of oak foliage (Meurisse et al., 2012). Furthermore, higher temperatures and drier conditions in spring and summer may accelerate larval growth, reducing larval mortality and so outweigh the negative effects of the increased mismatch. This might explain the observed increase in the population density of *T. processionea* in many European countries since the end of the last century (Van Oudenhoven et al., 2008). Finally, global warming may lead to a mismatch with higher trophic levels (Durant et al., 2007). Thus, further studies on the effect of climate change with special focus on *T. processionea*'s antagonists are needed to fully understand the increased frequency of outbreaks over the past 2–3 decades and to reliably predict this species' population dynamics in the future.

Nevertheless, it might be possible to use the equation to predict the time of egg hatch of *T. processionea* in ecological models and in monitoring programmes, which are used to estimate the most appropriate time to spray solutions containing entomophagous nematodes (Franssen, 2013) or biological plant protection agents like *Bacillus thuringiensis kurstaki*. It is still an open question, however, whether this method is reliable when the number of degree-days and frost days fall outside the range recorded in this study and when used in other parts of *T. processionea*'s geographic range.

ACKNOWLEDGEMENTS. We are deeply indebted to L. Henke for technical support, S. Krautzberger and S. Mösch for practical assistance and H. Schröter and H. Bogenschütz for their expert advice. Last but not least, we would like to thank the unknown reviewers for their helpful comments on previous versions of the manuscript.

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Received November 11, 2013; revised and accepted January 15, 2014
Prepublished online March 27, 2014