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ÜBERSICHTSARTIKEL

# Five years of continuous *Thaumetopoea processionea* monitoring: tracing population dynamics in an arable landscape of south-western Germany

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**Abstract** Within this paper we summarize the results of the *Thaumetopoea processionea* monitoring at two observation sites and try to interpret population dynamics from 2006 to 2010 considering meteorological data. Furthermore, observations on the behaviour of neonates associated with oak budburst are presented and discussed. In 2007 large larval colonies occurred and population densities peaked. Massive defoliation and larval migration due to food shortage were observed regularly leading to reduced female moth fecundity. Unfavourable weather conditions probably abetted OPM population decline in spring 2008. Additionally oak budburst was delayed remarkably. More detailed observations on the hatching process and the behaviour of single colonies revealed increasing mortality after two and a half weeks of starvation. The 2009 results indicated another increase of population densities, but exceeded cool and humid weather conditions in May 2010 presumably prevented a new OPM outbreak. In accordance with previous studies egg parasitisation seems to play a minor role in OPM population dynamics.

**Keywords** *Thaumetopoea processionea* · Oak Processionary Moth · Monitoring · Population dynamics · Neonates · Egg mortality

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## Fünf Jahre kontinuierliches *Thaumetopoea processionea* – Monitoring: Überwachung der Populationsdynamik in einem landwirtschaftlich geprägten Raum in Südwestdeutschland

**Zusammenfassung** In der vorliegenden Arbeit werden die Ergebnisse des an zwei Untersuchungsorten von 2006 bis 2010 durchgeführten *Thaumetopoea processionea* – Monitorings zusammengefasst und es wird versucht, die Populationsdynamik vor dem Hintergrund der Witterungsverhältnisse zu interpretieren. Des Weiteren werden Beobachtungen zum Verhalten der Eiraupen im Zusammenhang mit dem Eichenaustrieb dargestellt und diskutiert. Die Populationsdichte erreichte im Jahr 2007 ihren Höhepunkt, der durch große Raupenkolonien und starken Raupenfraß gekennzeichnet war. In der Folge wurde bei adulten Weibchen eine Reduktion der Fruchtbarkeit registriert. Im Frühjahr 2008 ging die Populationsdichte vermutlich aufgrund ungünstiger Witterungsverhältnisse deutlich zurück. Weiterhin kam es zu einer auffälligen Verzögerung des Eichenaustriebs. Detaillierte Beobachtungen zum Schlupfprozess und zum Verhalten einzelner Kolonien ergaben eine erhöhte Mortalität der Eiraupen nach zweieinhalb bis drei Wochen ohne Nahrungsaufnahme. Die Ergebnisse im Jahr 2009 ließen einen erneuten Anstieg der Populationsdichte erwarten, jedoch verhinderte vermutlich andauernde kühl-feuchte Witterung im Mai 2010 einen erneuten Populationsanstieg. In Übereinstimmung mit früheren Untersuchungen ist davon auszugehen, dass die Eiparasitierung bei der Populationsdynamik des Eichenprozessionsspinners eine untergeordnete Rolle spielt.

**Schlüsselwörter** *Thaumetopoea processionea* · Eichenprozessionsspinner · Monitoring · Populationsdynamik · Eiraupen · Eimortalität

## Introduction

*Thaumetopoea processionea* L. (Lep., Notodentidae), the so called oak processionary moth (OPM), is a univoltine lepidopteran species (Eckstein 1915) which is widely distributed in many parts of western, central and southern Europe (Panel on Plant Health 2009). The gregarious living larvae feed on different oak species. According to mass outbreak observations, the larvae are known to be serious defoliators of single oak trees within open landscapes (Nüßlin and Rhumbler 1922) and also of oak dominated forest stands (Zillig 1938; Jupe 1956; Skatulla and Lobinger 2006; Roversi 2008). Complete larval development has six stages. From the 3rd instar on the larvae produce minute urticating hairs which have high potential for causing serious allergic human health problems (Lamy et al. 1988; Bosma and Jans 1998; Maier et al. 2003). Fifth and 6th instar colonies build typical larval nests which serve as protective areas during resting times, moulting and pupation (Maksymov 1978).

Reports on *T. processionea* in Germany date back to the late eighteenth (Jupe 1956) and the early nineteenth century (Eckstein 1915; Offenberg 2000). First records for south-western Germany from the nineteenth century are listed in Ebert (1994). Although there have been several notices on local massive outbreaks in Germany within the nineteenth and the first half of the twentieth century (Eckstein 1915; Zillig 1938; Maksymov 1978), many observations indicate an overall increase of OPM abundances and an enlargement of the infestation areas since the 1990s (Feemers and Schmidt 1997; Flemming 1997; Kontzog 1998; Skatulla and Lobinger 2006; Lobinger 2008; Lehmann 2009). A similar trend was observed for south-western Germany (Bogenschütz 1998a; Delb and Veit 2006; Delb et al. 2008). Therefore, several control measures have been taken using *Bacillus thuringiensis* var. *kurstaki* (*B.t.k.*) agents from 1996 to 2009 to avoid human skin irritations in highly frequented public places and to protect infested oak stands from repeated defoliation (Bogenschütz 1998a; Bub et al. 2005; Schröter et al. 2009a, b). In south-western Germany infestation mainly occurs in the wine-growing regions 'Oberrheinisches Tiefland' and 'Neckarland'. Due to increasing numbers of infestation incidents the monitoring of the population status of *T. processionea* has been intensified in order to retrace and interpret population dynamics of this oak pest.

## Methods

### Study area

Two monitoring sites with an approximate distance of 10 km were selected to gain information on local populations and the developmental status of *T. processionea*. Both sites are located in the favourable climate of the Upper Rhine Valley close to Freiburg i. Br. ($T_{annual}$=11.07°C, precipitation sum 914.8 mm p.a.[1]) within open and agricultural landscapes. Without exception all investigations were conducted on pedunculate oak trees (*Quercus robur* L.). Monitoring site 1 is located near Hausen a. d. Möhlin. The planted oak trees are 6 to 18 m high with diameters of 16 to 55 cm at breast height. They partly alternate with sycamore maple trees (*Acer pseudoplatanus* L.) forming an alley extending to 1.5 km. The local OPM population was first noticed in the beginning of the 1990s. No control measures have been taken within the past five years. At monitoring site 2 planted oaks are 7 to 8 m high with diameters of 14 to 23 cm at breast height and forming spacious hedgerows. The local OPM population was detected there in 2007.

### Monitoring programme

The monitoring programme comprised the recording of neonate hatching dates, the estimation of female moth egg laying activity and fecundity, the degree of defoliation of oak trees as well as the infestation level of larvae and male moth flight activity. ***Neonate hatching*** was determined by continuous surveys of marked egg batches in 2008, 2009 and 2010 at both monitoring sites. ***Egg laying activity*** and ***fecundity*** of the female moths was determined at monitoring site 1 by identifying fresh egg masses as well as counting the number of eggs per batch on 20 one metre long shoots representing all parts of the upper crown from three sampled oak trees (Bogenschütz 1998a). The degree of oak defoliation and encountered numbers of larvae or nests were important indicators for the assessment of population densities and infestation levels during larval development. The ***extent of defoliation*** was categorized as very low (<10%), low (10–30%), medium (>30–60%) and heavy (>60%). ***Larval*** and ***nest densities*** were estimated using both the abundance and size of the colonies as well as the nests. At monitoring site 1 ***flight activity of male moths*** was surveyed from mid-July to the beginning of September using five masts bearing two fixed delta-shaped traps each at a height of 3 and 7 m above ground level equipped with pheromone devices (Temmen GmbH). The dispensers were only replaced in case of loss. In 2008, PET-bottles with a small slit filled with soap solution as preserving agent were used instead of delta-shaped traps. In mid-August 2006 pheromone traps were used for two and a half weeks. Additionally four 15 W black light traps were run at monitoring site 1 for two weeks in mid-August 2006 and for five weeks from the end of July until the end of August in 2007 respectively. Weather data were obtained from the meteorological station 'Mengen' which is

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[1] Long-time average from 1961 to 2010 based on weather data provided by the DWD for the meteorological station 'Freiburg'.

run by the LTZ Augustenberg located 3.8 km from site 1 and 6.4 km from site 2 respectively.

### Hatching rate and egg mortality in laboratory

In mid-January 2010 16 fresh egg batches from each monitoring site were collected to determine egg mortality, parasitisation, hatching time and hatching rate. After counting the number of eggs per batch they were placed in plastic Petri dishes and stored in dark conditions at +2.0°C, which marks neonates' thermal threshold for development (Custers 2003). On February 3 all eggs were transferred to a climate chamber with a light/dark regime of 13/11 hours; mean daily temperature was set to 18°C. The batches were observed daily for neonates' hatching activity and emerging egg parasitoids until March 11. From March 11 to the end of July the batches were kept under average room temperature and natural light conditions. They were again examined twice for egg parasitoids and late coming neonates on April 15 and July 8. At the end of July all still closed eggs were dissected to determine sterile eggs which can be identified by orange coloured, dried-up yolk (Tsankov et al. 1998).

### Oak budburst, larval hatching and larval development in 2010

The degree of defoliation and the predominant larval stage as well as the intensity of the OPM larval infestation were regularly surveyed on 23 oak trees at monitoring site 2. From 18 of these oak trees the twigs of the lowest third of the crown were surveyed for fresh batches on March 17. Overall 85 egg masses were marked on 16 trees in order to investigate daily neonate hatching from March 24 to April 9. Simultaneously the status of the buds of each monitored tree was assessed and classified as "closed", "swollen", "burst" or "foliated". From April 9 to April 30 the developmental stage and behaviour of single larval colonies were surveyed on all 23 trees every second day. Until July 9 the lower parts of the crowns were inspected weekly for the determination of the larval developmental status in different colonies and trees. If there was more than one larval stage present on a single tree, intermediate stages were defined for that tree. If all larvae of a single tree were in the feeding phase of the 2nd instar, developmental status was defined as 2.0 for that tree. In case they were shortly before moulting into the 3rd instar, the status was 2.25 and once the first larvae were in the 3rd instar, the status was 2.5. If many larvae attained the 3rd instar and some were still in the 2nd instar shortly before moulting, the developmental status was defined as 2.75.

### Statistical analyses

Differences in egg batch density on surveyed oak twigs were calculated using $\chi^2$-test for 2006 to 2009 assuming equal distribution (null hypothesis). In case of significance, those single $\chi^2$-values for each year that exceeded 3.84[2] were considered to make a significant contribution on 0.05 level. The nonparametric Kruskal-Wallis method followed by the Tukey-Kramer procedure for multiple comparisons (Sachs 1992) was used to differentiate the mean number of eggs per batch for all four monitoring years.

Spearman's rank correlation coefficient was calculated to assess the impact of timing of bud opening on the present larval developmental status on monitored oak trees at different times of larval development. A Bonferroni-Holm correction was used to maintain the global 0.05 level. Data analysis was run with SPSS (version 11.5) or self-programmed tests.

## Results

### Field observations from 2006 to 2010

Numerous trees were infested in 2006 but the number of males caught with pheromone and light traps in summer that year was rather low probably due to the short exposure time of the traps. Anyhow pupation nests of different size that outlasted the winter months indicated medium to high levels of OPM larval density in 2006 at monitoring site 1 (Table 1). In spring and summer 2007 OPM population density was at its current maximum. Huge larval aggregations consisting of hundreds of animals caused severe defoliation on many oak trees (Table 1). Furthermore colonies of 5th and 6th instar larvae were observed emigrating from completely defoliated trees, some of them starving in arable fields nearby. The same situation was observed at monitoring site 2 that year. Extensive catches of male moths in late summer at monitoring site 1 also indicated high population levels (Table 1). But strongly decreased larval densities and low levels of oak defoliation were observed at both monitoring sites in spring and summer 2008. The number of males captured with pheromone PET-traps was nearly zero (Table 1). In summer 2009 larval densities and defoliation of oak trees increased again. In late summer that year the number of male moths caught in delta-shaped pheromone traps increased noticeably as well (Table 1). In early spring 2010, larval densities and the degree of oak defoliation remained on 2009 level, but trapping male moths resulted in lowered catches of 29.8% compared to 2009 (Table 1).

When comparing the number of fresh egg batches as well as the average batch size for the whole observation period a significant difference within both parameters was calculated (*egg batches:* $\chi^2$-test: df=4; $\chi^2$=20.8; $p<0.001$; *batch size:*

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[2] $\chi^2$-values exceeding 3.84 allow a rejection of the null hypothesis on 0.05 level when the degree of freedom is 1.

**Table 1** Results of the monitoring programme as well as meteorological and phenological data for the 2006 to 2010 period

| Monitoring year | 2006 | 2007 | 2008 | 2009 | 2010 |
|---|---|---|---|---|---|
| Date of neonate hatching | | | April 4 | April 6 | March 30 |
| Date of oak sprouting[a] | April 23 | April 16 | April 27 | April 22 | April 8 |
| Lack of coincidence [days][b] | | | 23 | 16 | 9 |
| April air temperature [°C][c] | −0.4 | +3.5 | −1.4 | +2.5 | +0.3 |
| April precipitation [mm][c] | +0.5 | −55.1 | +96.0 | −46.3 | −34.5 |
| Late frost days after hatching [min. temperature] | 5 [−3.3°C] | 1 [−0.8°C] | 2 [−5.6°C] | 0 | 5 [−2.9°C] |
| Larval and nest density[d] | ■■■̣[e] | ■■■■ | ■ | ■■ | ■□ |
| Degree of defoliation[f] | | ▲▲▲▲ | ▲ | ▲▲ | ▲▲ |
| Moths in 4 light traps | 40[g] | 500[h] | | | |
| Male moths in 10 pheromone traps | 35[g] | 1135 | 5[i] | 953 | 284 |
| Number of fresh egg masses | 17 | 23 | 4 | 16 | 5 |
| Trend of population development | ●● | ●●● | ● | ●● | ●○ |

[a] Phenological station "Grißheim", located in the Upper Rhine Valley 8 and 19 km distant from monitoring sites 1 and 2 respectively. Source: DWD

[b] Time span between neonate hatching and oak sprouting

[c] Deviation from the long time average (1994–2010); source: LTZ weather station 'Mengen'

[d] low: ■■ low to medium: ■■■ medium to high: ■■■■ high (huge colonies): ■■■■̣

[e] Larval densities in 2006 were estimated according to pupation nests in March 2007

[f] low: ▲, low to medium defoliation: ▲▲; low to sporadic high defoliation: ▲▲▲; medium to high defoliation: ▲▲▲▲

[g] In 2006 traps were disposed for two and a half weeks in mid-August

[h] The sex ratio of moths captured with light traps was 17.8% females and 82.2% males

[i] In 2008 PET-bottles were used instead of delta-like traps

Kruskal-Wallis-test: df=4; $\chi^2=25.6$; $p < 0.0001$). Assuming equal abundances more batches than expected were found in 2007, the year of mass propagation ($\chi^2=7.7$), and fewer than expected were found in 2008 and 2010 when population density decreased (2008: $\chi^2=6.2$; 2010: $\chi^2=4.9$) (Table 1). In 2007 the average batch size was observed to be significantly reduced compared to 2006, 2008 and 2009 (Tukey-Kramer: $p<0.05$) (Fig. 1).

In 2008 and 2009 neonate hatching occurred at the beginning of April whereas the first neonates in 2010 were observed at the end of March (Table 1). Conspicuously, April weather conditions in 2007 and 2009 were very warm and dry in contrast to a cool and rainy April in 2008. On the other hand, weather in April 2006 was close to long-time average temperatures and precipitation; whereas April 2010 was comparably dry (Table 1). May 2010 was reasonably cold ($T_{Dev.}=-2.7°C$) and rainy ($Prec_{Dev.}=+20.8$ mm) compared to the weather conditions in previous years. Within the whole observation period late frost incidents were slight and scarce (Table 1). Oak sprouting was earliest at the end of the first week in April 2010 and latest at the last week in April 2008 differing for 19 days. Hence, synchrony of neonate hatching and oak sprouting fitted best in 2010 and worst in 2008. Consequently, developmental time of first instar larvae was prolonged for one week comparing 2008 with 2009 and 2010. There were no observations for 2006 and 2007.

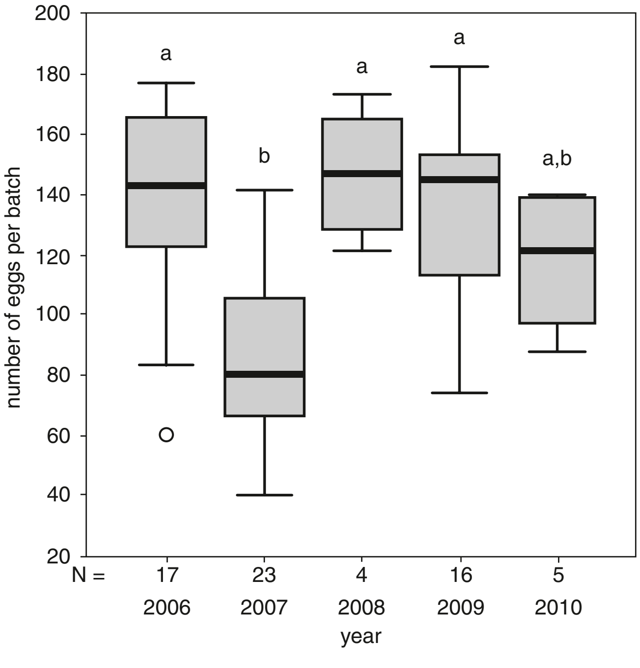

**Fig. 1** Average size of *T. processionea* egg batches found on *Quercus robur* from 2006 to 2010 at monitoring site 1. Different letters indicate significant differences on a 0.05 level after the use of the Tukey-Kramer method for multiple comparisons

### Hatching rate and egg mortality in laboratory

The mean hatching rate of OPM larvae from egg batches collected in January 2010 was on a high level, i.e. egg and

**Table 2** Hatching rates and causes of mortality for *T. processionea* egg batches (∅ = median). In January 2010, sixteen batches were collected from different oak trees at each monitoring site; the batches were reared under laboratory conditions in February

| Site | Eggs/batch | | | Hatching rate (%) | | | Parasitized eggs (%) | | | Parasitized batches (%) | Sterile eggs (%) | | | Dead neonates (%) | | | Destroyed eggs (%) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ∅ | Min | max | ∅ | Min | max | ∅ | min | max | | ∅ | min | max | ∅ | min | max | ∅ | min | max |
| 1 | 145 | 74 | 182 | 93.1 | 42.3 | 100 | 2.0 | 0 | 9.6 | 68.8 | 0.7 | 0 | 5.8 | 1.4 | 0 | 37.5 | 0 | 0 | 5.5 |
| 2 | 160 | 126 | 209 | 94.7 | 66.4 | 99.4 | 1.2 | 0 | 14.6 | 62.5 | 0.6 | 0 | 13.1 | 2.2 | 0 | 16.8 | 0 | 0 | 2.5 |

neonate mortality was very low (Table 2). The neonates from both monitoring sites hatched rather synchronically and hatching peaked within one or two days (Fig. 2).

Besides egg parasitism, sterility or the failure of neonates to hatch were reasons for non-eclosion (Table 2). Non-fertilized OPM eggs were found in 62.5% of the surveyed batches, but overall sterility rate was on a low level. More than 60% of all batches were parasitized; maximum parasitism rate was 14.6%. Generally, two different species of egg parasitoids were found, 94.5% of the specimens were *Anastatus cf. bifasciatus* (Eupelmidae) males and 5.5% belonged to the Encyrtidae familiy. Parasitoid eclosion occurred after OPM neonate hatching through small lateral holes. Some of the fully developed parasitoids died inside the OPM egg shell, the same accounts for neonate larvae which were found dehydrated inside the egg shells. Single lateral eggs were observed to be destroyed probably due to feeding of tits or treecreepers (Dingler 1927).

## Oak budburst, neonate hatching and larval development in 2010

At monitoring site 2 first larvae hatched on March 30. From March 31 to April 6 cold and rainy weather conditions prevailed, so further hatching was delayed. During this period the already hatched neonates ($n=13$) stayed quiescent on their batches for four days on average (min: 1 day; max: 7 days). Due to increasing temperatures and dry weather peak hatching occurred on April 7 and 8 lasting one to two days per single batch, resembling hatching behaviour observed in the laboratory. Colonies that hatched under these favourable weather conditions ($n=47$) stayed on their batches for one day on average (min: 0 days; max: 2 days). Subsequently the colonies moved to shoots or buds up to 60 cm distant from their batches. First aggregations of different colonies already occurred on heavily infested trees. Furthermore, colony movements and feeding activities could be observed regularly during daytime. When approached buds were still closed the colonies moved on to other buds mostly within 1 or 2 m distance. When the buds swelled the 1st instar larvae penetrated and started feeding inside the buds, moving to a new bud nearby when the former one was completely consumed. Caved buds as well as stout neonates—probably due to water intake—were conspicuous signs for first food intake. The date of first-time feeding was strongly dependant on the host trees' budburst timing. A maximum deviation of 20 days concerning budburst could be observed among the sampled trees. When the neonates hatched the buds of the earliest sprouting oaks started to burst while those of most trees were still closed. Since there was no obvious relation between the date of neonate hatching and host tree's budburst, single neonate colonies had to endure up to three weeks before first food intake. When asynchrony of hatching and budburst accounted for single days only, feeding started shortly after the emergence of the neonates. But in most cases the neonates could be observed starving one up to two and a half weeks on closed buds before first-time feeding. On the other hand, the larvae of single continuously surveyed colonies died after 16 to 20 days without any food ingestion on late sprouting oaks. Close to dieback these colonies showed signs of retarded motion, desiccation and disintegration (Fig. 3a). Besides, some colonies that survived on late sprouting oaks were of small size when the neonates started feeding (Fig. 3b). At the end of May and in June, larval abundance decreased within the whole monitoring area. Thus, overall defoliation was on a low level (median: 5%).

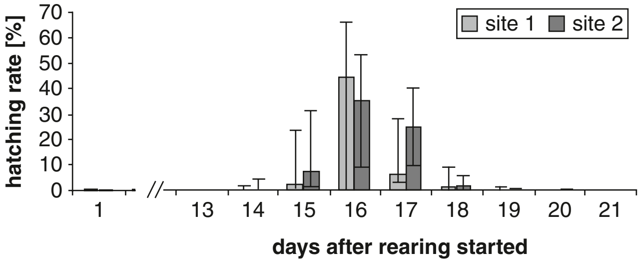

**Fig. 2** Medians and quartiles for the daily hatching rates of OPM neonates derived from both monitoring sites (each with 16 batches) and reared in laboratory

Larval hatching on different trees occurred rather synchronically, so on April 8 most of the neonates were already present on the surveyed trees (Fig. 4a). Two weeks after peak hatching some colonies feeding on the early sprouting trees had already moulted into the 2nd instar while colonies on trees with a delayed budburst had hardly developed (Fig. 4b). A strong statistical correlation between current larval stages and the date of host trees' budburst was confirmed for observations another two (Spearman's Rank Correlation: $\rho^2=0.787$; $p<0.0001$; Fig. 4c), four ($\rho^2=0.667$; $p<0.0001$; Fig. 4d) and seven ($\rho^2=0.872$; $p<0.0001$; Fig. 4e) weeks later. Consequently three different larval instars were present simultaneously on surveyed oak trees within the moni-

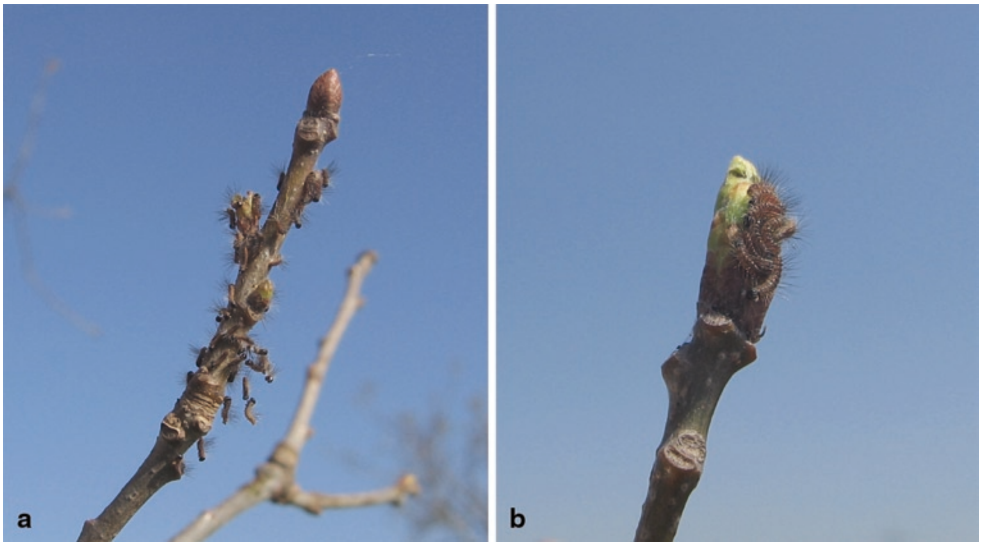

**Fig. 3** First instar *T. processionea* colonies on oak trees with a delayed budburst in 2010 at monitoring site 2: **a** dissolving neonate colony after 16 days of starvation on April 24, **b** small sized colony of already fed 1st instar larvae on April 28

toring area on May 7 and 21. The first pupae were observed at the beginning of July. The flight period started on July 23 and ceased on August 27. The dissection of several egg batches revealed that embryonic development starts shortly after oviposition and that first neonates were already present inside the egg shells at the beginning of September.

## Discussion

Custers (2003) constitutes that OPM has been observed to be an eruptive pest in the Netherlands in the nineteenth century. Long periods of low population densities were interrupted by massive outbreaks and subsequent breakdowns. Gradations reported in Maksymov (1978) lasted one to six years whereas the current OPM gradation in the federal state of Brandenburg is evolving rather chronically (Lehmann 2009). Though numerous OPM gradations have been described so far, underlying factors for outbreaks and breakdowns are not always known in detail. Generally, food quality and plant-herbivore-interactions, natural enemies as well as intra- and interspecific competition are important biotic factors inducing fluctuations in insect populations. Among abiotic factors, weather conditions—primarily temperature and precipitation—play a major role in insect population dynamics (Schwerdtfeger 1981). Delb et al. (2008) reported high infestation levels from 1995 to 1997 for Baden-Württemberg followed by a repeated increase of OPM abundances after the extremely hot and dry weather conditions in summer 2003. Even though there is no detailed comparable data for the selected monitoring areas of this study prior to summer 2006 and spring 2007 respectively, it can be assumed that infestation levels and population dynamics developed likewise in these areas. Nest densities indicated a rather high level of OPM abundances in 2006 but the number of trapped moths in late summer 2006 was low. The results do not comprise the whole flight period because the traps were exposed for two weeks only when weather conditions were cool and rainy. Exceeding warm and dry weather conditions in April 2007 were very appropriate for early larval development and apparently contributed to low mortality levels, obviously promoting the observed mass propagation of OPM larvae and severe oak defoliation at both sites. The current peak of population densities in 2007 was a phenomenon not only within both monitoring areas but also applies to many parts of Baden-Württemberg's oak forests with OPM infestation (Wagenhoff and Delb 2011 submitted). Grison (1952) already noted that warm and dry springs precede OPM outbreaks. Offenberg (2000) and Van Oudenhoven (2008) also assume warm and dry weather conditions to abet OPM mass propagations. Wellenstein and Schwenke (1978) remark that warm and dry periods result in comparably higher sugar contents of the leaves which in turn leads to a more rapid development and lower mortality in *Lymantria dispar* L. larvae. It can be assumed that this also accounts for OPM larval development.

The OPM population parameters consistently indicated a population collapse in 2008. But trapping results in late summer 2008 were uncertain since a different trapping method was applied. However, the use of PET-traps in OPM monitoring had been successful in a Bavarian survey (Lobinger 2010, pers. com.). It can be assumed that for the present survey disposed pheromone dispensers did not bias the capture rates notably since they were used effectively in 2007 and 2009 with delta-shaped traps. Therefore we conclude that also population decline did contribute to the low pheromone trap catches.

For 2007 food shortage, migration and parasitisation of the larvae were observed but altogether these factors can not solely account for the dramatic population decline in

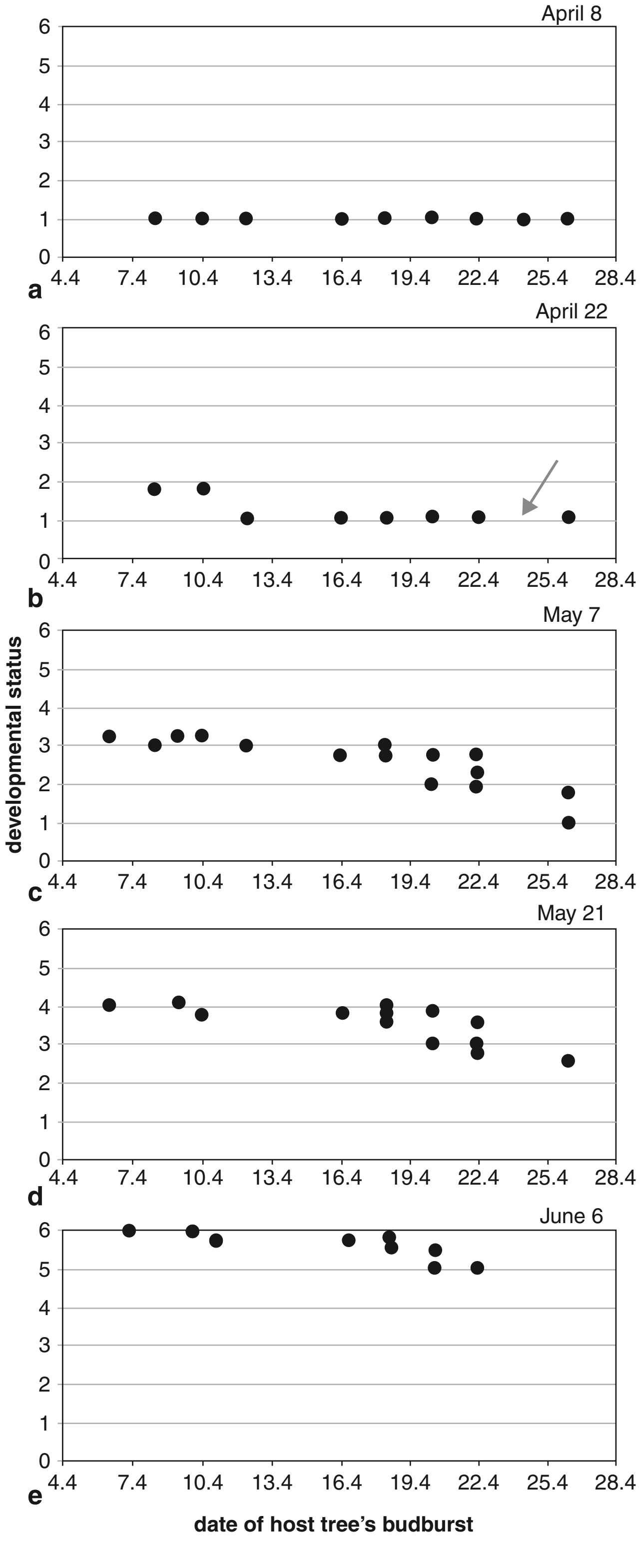

**Fig. 4** Chronological sequence of the developmental status of larval colonies present on surveyed oak trees depending on host trees' budburst: **a** 16 trees, **b** 15 trees (due to colony disappearance on a late sprouting tree [*arrow*]), **c** 20 trees (due to increasing larval size colonies on another five trees were detected), **d** and **e** 16 trees (due to colony disappearance on some of the sampled trees). Overlapping dots are the reason for differences in given sample sizes and the number of dots shown in the graph. Developmental statuses see '*Methods*'

2008. Moreover male moth catches as well as female egg laying activity suggested even progression of mass outbreak in 2008, although weather conditions during flight and reproduction were unfavourable in late summer 2007. Ichneumonids, Braconids and Tachinids could be encountered regularly close to OPM nests and colonies, but maximum parasitisation rates cited in literature did not exceed 20% to 30% (Bogenschütz et al. 1988; Tschorsnig 1993; Stigter et al. 1997; Bogenschütz 1998a). Stigter et al. (1997) also state, that intensive agricultural activities including insecticide use are noxious for natural enemies' reproduction and survival. Spiders and ants are known to attack early larval stages of *Thaumetopoea pinivora* Treitschke (Ronnas et al. 2010). Different species of spiders were regularly observed on oak twigs at both monitoring sites together with OPM neonates but their impact on OPM neonate mortality is unknown. Altogether, it can not be assumed that the occurrence of larval predators and parasitoids caused population collapse in both surveyed areas. In line with previous studies (Wiese 1990; Stigter and Das 1996; Flemming 1997; Bogenschütz 1998a; Mirchev et al. 2003; Roversi et al. 2005; Möller 2006; Skatulla and Lobinger 2006), current results indicate low levels of egg mortality, sterility and parasitisation in *T. processionea* populations. The results of the 2010s egg survey resembled the findings of Dissescu and Ceianu (1968) in Romania where a maximum of 15.5% of the eggs were parasitized by *Anastatus bifasciatus* Geoffroy. Tiberi and Bin (1988) observed parasitisation levels between 2% and 5% for *A. bifasciatus* in Italy. The Encyrtid *Ooencyrtus masii* Mercet and *Trichogramma sp.* were also reared from OPM eggs but parasitisation rate was even lower compared to *A. bifasciatus* (Tiberi et al. 1991). Therefore, egg parasitisation is unlikely to account for 2008s population decline. Microsporidian protozoa are common pathogens in OPM populations (Hoch et al. 2008) but a collapse due to their occurrence has not been reported yet. Additionally, epizootic diseases are thought to predominately kill the latest instars of an insect pest (Biliotti 1959; Woods and Elkinton 1987; Choate and Rieske 2005) while 2008s OPM population decline was observed during early larval development already. Consequently, pathogens are not considered to be responsible for the observed population collapse too. The role of host-plant interactions in 2008s population decline could not be excluded according to the findings of Battisti (1988) for *Thaumetopoea pityocampa* Denis & Schiffermüller. But for OPM and its host trees, data on this topic are still lacking.

Presumably an obvious reduction of female fecundity during mass propagation in 2007 assessed by counting the number off eggs per batch contributed to OPM population decline in spring 2008. Roversi (2008) noticed a similar phenomenon in the year preceding population collapse. Overpopulation followed by food shortage lead to reduced female fecundity in *Thaumetopoea solitaria* Freyer (Halperin 1983). According to own observations, single 5th instar OPM larvae could be found pupating prematurely after severe defoliation. Since all eggs are fully developed with adult female eclosion (Maskymov 1978), required nutrition for egg development has to be ingested by the final larval instars. Resembling other lepidopteran species (e.g. Schütte 1957), fecundity in the genus *Thaumetopoea* strongly depends on food intake of the female larvae (Douma-Petridou 1990). Consequently larger sized pupae carry more eggs in the subsequent adult stage than small pupae (Dissescu and Ceianu 1968). Therefore, we assume 2007s mass propagation to have caused reduced reproduction rates abetting population decline in 2008. Besides reduced fecundity, unfavourable weather conditions during April when the young larvae had already hatched are thought to have played the major role in 2008s population collapse. In north-eastern France, late frost events in spring destroyed the freshly flushed leaves and caused sudden population decline in 1997 (Custers 2003), but this doesn't apply to the present survey. Generally, early larval stages of exophytic insects are more susceptible to weather induced mortality than later instars (Schwerdtfeger 1981; Cornell and Hawkins 1995). Furthermore, early larval stages are considered to play a key role in determining population sizes, as they are very sensitive and therefore suffering high mortality rates (Hodar et al. 2002; Zalucki et al. 2002). For Germany's southern part of the Upper-Rhine-Valley, OPM neonate hatching has been noted at the end of March or the beginning of April in the past years. This corresponds closely to the observations of early hatching dates at the end of March in eastern France (Custers 2003). In contrast to *Operophtera brumata* L. (Van Dongen et al. 1997) the neonates are known to hibernate fully developed within their egg shells (Biliotti 1952). Hatching occurs rather simultaneously in spring with little temporal variability, which is in line with previous findings (Biliotti 1952; Pascual 1988; Roversi 2008). Furthermore, hatching has been noted to precede *Q. robur* budburst which might be an adaptation to ensure, that the neonates start feeding on predominantly fresh and soft leafs containing high amounts of protein and far less tannin (Feeny 1968, 1970; Jones and Despland 2006). But unlike *L. dispar* (Schedl 1936; Van der Linde 1971), the gregarious and oligophagous *T. processionea* neonates do not spread by wind flow which puts crucial group coherence at a very high risk. Furthermore, 2010s observations indicate that neonate colony movement prior to feeding generally occurs within a range of only few meters. Consequently, neonates have to survive several days or even weeks on their host tree until the buds flush and feeding is possible, especially on late sprouting specimen or in years with a delayed budburst like in 2008. Present observations contribute to previous findings (Stigter et al. 1997; Custers 2003) that OPM neonates are generally adapted to asynchrony of hatching and budburst, since they are able to survive in a quiescent condition for two or three weeks without any food consumption. But even in years with a wide spread overall coincidence like in 2010, single colonies could be observed dying of starvation or being decimated on late sprouting oaks. Therefore, we conclude that the extensive asynchrony in 2008 caused neonate mortality and the onset of population decline. This agrees with the statement of Custers (2003) relating population decline to an asynchrony minimum of 18 days. As hatching precedes budburst in our region and neonate survival is limited to two or three weeks without any food ingestion, late sprouting oaks can be expected to be less infested and also defoliated, especially in years with a poor coincidence. Further studies should try to prove if this accounts for the high variability of defoliation among different oaks noticed even in heavily infested stands (pers. obs.). Besides asynchrony, prevailing cool and rainy weather itself presumably caused high mortality among the neonates in April 2008. Extended periods of rain are known to effect high mortality and therefore impairing population development in OPM (Grison 1952; Jupe 1956). Laboratory studies revealed that neonate surviving time is extended when temperatures are low (unpublished data). Anyhow the immediate effect of rainy weather might have been more important for mortality than delayed budburst, since temperatures were rather low during the time of asynchrony.

Nevertheless, current observations have shown that timing of oak budburst has an important impact on the duration of larval development. It begins when the neonates start feeding, leading to an advanced development on earlier sprouting trees. High larval mortality rates on late sprouting trees will result in smaller colonies and Ronnas et al. (2010) have shown that small *T. pinivora* colonies have reduced growth rates leading to a delayed development. Therefore, colony size might have influenced developmental time too. Since it is well known that there is a high variability in leaf flush among different trees within pedunculate oak stands (Krahl-Urban 1959), several different instars might be present on different trees within the same stand at the same time. This has to be noticed when applying plant protection agents like *B.t.k.*, whose efficiency strongly depends on specific larval stages.

Summarizing reduced fecundity and unfavourable April weather likely having been two reasons for 2008s population decline, both factors might have been interacting. Reduced fecundity will lead to smaller colonies, which are known to have lower thermal gains and reduced growing rates in *T. pinivora* (Ronnas et al. 2010). Hence, the prolongation of neonate development may enhance the susceptibility to biotic or abiotic factors (Aimi et al. 2008). Besides all mentioned mortality factors there might have been an influence of maize plant protecting agents on the basis of

Clothianidin which cannot be excluded. At the end of April 2008, Clothianidin was applied in Baden-Württemberg to prevent maize seed from damage of Western corn rootworm (*Diabrotica virgifera virgifera* LeConte). Although findings after the flight period 2008 indicated low levels of egg laying activity, larval abundance increased in 2009 compared to the previous year. This was probably due to the favourable weather conditions and the short period of asynchrony between neonate hatching and oak budburst in spring 2009 causing little mortality among the larvae. Male moth catches and egg batch densities indicated rising population levels again, but no mass propagation was observed in 2010 although hatching synchrony with budburst was very advantageous. Subsequently weather conditions in May were very cool and rainy, likely effecting high mortality and preventing a new mass propagation. In autumn male moth trap catches and egg batch densities were on a rather low level corroborating the observations of population decline during spring 2010.

Although the results of the current survey indicate a relation between all monitoring methods when reconstructing population dynamics in OPM, a reliable system for mass outbreak forecast with adequate warning thresholds is still lacking. Estimating egg batch densities and larval abundances is time-consuming and expensive. Furthermore, pheromone trapping has essential prerequisites described in Bogenschütz (1998b) which are difficult to be implemented. But even with a reliable early-warning system, the prognosis has to be verified during the critical phase of early larval development and oak sprouting in early spring. The analysis of 2007/2008 and 2009/2010 have shown that the predictions of population development in spring would have failed. Nevertheless, monitoring of OPM larval hatching and development as well as sprouting of oaks was seen to be sufficient for the determination of the favourable time for the application of plant protection agents (e.g. *B.t.k.*).

Although some aspects of OPM biology and population dynamics are getting quite consistent, many questions still remain unanswered. OPM-oak-interactions, the role of OPM in oak decline, the impact of global warming on OPM abundance and distribution as well as the impact of natural enemies on OPM populations should be focused on in further investigations.

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