

Deliverable summary D4.2
Surveillance of damage by specific pests based on optical and chemical signals

Project acronym:	**HOMED**
Project full title:	**Holistic Management of Emerging forest pests and Diseases**
GA n°:	**771271**
Start date of the project:	**October 1st 2018**
Duration:	**48 months**
Project coordinator:	**Herve Jactel (INRA)**
Planned delivery date:	**M30**
Actual submission date:	**M30**
Workpackage:	**WP4**
WP leader:	**UNIPD**
Lead beneficiary:	**UNIPD**
Partners involved:	**UQ**
Version:	**01**

Dissemination Level	
PU Public	**PU**
CI Classified, as referred to Commission Decision 2001/844/EC	
CO Confidential, only for members of the consortium (including the Commission Services)	

Table of contents

1. Summary 3

2. Introduction 3

3. Results 4

3.1. Result 1 4

3.2. Result 2 5

3.3. Result 3 8

4. Conclusions 11

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

1. Summary

Objectives:

The general aim of the deliverable was to provide a methodology for the identification of visual cues associated with the larval behaviour of the processionary moths. Forest and urban trees will be considered, in relation to the risk of exposure of humans and animals to the urticating setae produced by the larvae in Europe and Australia.

Rationale:

The model chosen for the deliverable was the processionary moths, with several species occurring in Europe and in Australia that share the same life history and are important defoliating insects and represent a health threat to humans and animals because of the release of urticating setae. The approach was based on visual cues associated with the larval behaviour, which provided reliable results that are presented in this report.

Teams involved:

UNIPD – coordination and application in Italy

UQ – application in Australia

2. Introduction

Pest insects are defined as organisms that cause harm to humans, animals, crops or property (Dent, 2000). One of which includes gregarious caterpillars with urticating hairs (setae), specifically *Thaumetopoea pityocampa* and *Ochrogaster lunifer* found in Europe and Australia, respectively. The setae from the larvae are released by disturbance and/or mechanical stimulation and are harmful to humans and animals in several ways; including urticaria and allergic reactions in humans, tongue necrosis in dogs (Mullen and Durden, 2009), and miscarriages in horses (Cawdell-Smith *et al.*, 2012). Humans and animals can be exposed to urticating setae by direct contact with larvae, indirectly via the environment (e.g. on the ground and carried by wind), and by ingestion through contaminated feed and water (Mullen and Durden, 2009). Therefore, the containment of this species is highly important because of these life-threatening health concerns and economical damage.

Thaumetopoea pityocampa larvae are destructive defoliators of pine and cedar trees in the Mediterranean Basin and Southern Europe (Zamoum, Martin and Bensidi, 2015). *Thaumetopoea pityocampa* larvae feed throughout winter until spring in northern Italy, when the final instar larvae leave their tent (nest) in the canopy and descend to the ground to find a pupation site (Robredo, 1963).

Ochrogaster lunifer is a widespread univoltine species found across coastal and inland Australia where its *Acacia*, *Eucalyptus* and *Corymbia* spp. host trees occur (Perkins *et al.*, 2016; Steinbauer, 2018). In outbreak years, this species defoliates host trees and establishes new colonies where hosts are present (Floater and Zalucki, 1999). The larvae feed throughout the summer until they reach their final instar in autumn, when they leave their nest permanently in search of a suitable pupation site underground. After emerging from the pupa, female moths deposit eggs at the base of a host tree trunk and cover them with urticating scales from their abdomen (Perkins *et al.*, 2016). The urticarial nature of both the larvae and adults makes their physical removal for pest control difficult and creates an occupational health and safety risk.

The objectives were to investigate and determine the unknown behavioural movements of *O. lunifer* and *T. pityocampa* and compare their morphological, physiological, and ecological drivers. The project focused on quantitative observational and experimental data associated with pre-pupation procession movements,

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

larval vision, dispersal within host trees and social organisation of larval colonies. Knowledge of dispersal, physiology and behaviour in these important pest species will facilitate building models to predict exposure risk and application of pest management strategies.

3. Results

1. **Result 1: Ground dispersing behaviour of processionary caterpillars from Europe and Australia and their associated risks**

   Published as: Uemura M., Perkins L.E., Zalucki M.P., Battisti A. 2020. Movement behaviour of two social urticating caterpillars in opposite hemispheres. Movement Ecology 8:4 doi.org/10.1186/s40462-020-0189-x

Methods

Each year from March to May, *O. lunifer* and *T. pityocampa* caterpillars leave their nesting sites and form head-to-tail processions on the ground in search of pupation sites. This pre-pupation procession behaviour and its associated risk of human contact with *O. lunifer* and *T. pityocampa* caterpillars were studied and compared in Australia and Italy, respectively. *Ochrogaster lunifer* processions were followed from various *Acacia* spp. host trees at The University of Queensland (UQ), Gatton campus, Queensland, Australia (-27°56' S, 152°34 E). The campus is a semi-urban environment with buildings and patches of vegetation throughout. For *T. pityocampa* processions, the field sites were at three pine forests in Veneto, Italy: Monte Garzon (45°30' N, 11°11' E), Precastio (45°31' N, 11°10' E) and Carbonari (45°32' N, 11°10 E). The selected field sites are planted forests for soil conservation and are also used for recreational purposes such as hiking, cycling and picnics. The distance, duration, orientation and response to visible light of the pre-pupation processions were studied in both species to determine general patterns.

Results

In the morning, *O. lunifer* and *T. pityocampa* processions travelled on average 40 and 16 m per day from the nest in 153 and 223 min respectively, in search for potential pupation sites. *Ochrogaster lunifer* pre-pupation processions travelled generally to the north or south when leaving the nest, as was their final orientation to the bivouac/pupation site (Fig. 1a and b). Whereas *T. pityocampa* processions had no preference in orientation (Fig. 1c). The orientation preference/absence could be explained by the light preference by the leading larvae of both species. *Ochrogaster lunifer* larvae orientated towards darker areas while *T. pityocampa* orientated towards lighter areas of the environment for potential pupation sites. At the Australian field site, it is generally warmer at this time of year and host trees were patchy with a lot of clearings. Therefore, orienting more to the north or the south could avoid direct sunlight which came from the east to the west. Italian field sites were cooler because of the homogenous dense pine forest, and lighter areas are restricted to footpaths and nearby meadows. Therefore, *T. pityocampa* larvae searched for sunny exposed soil in gaps and edges of forests for optimal pupae survival (Dulaurent et al. 2011, Jactel *et al.*, 2015).

During our observations, 27% of *O. lunifer* and 44% of *T. pityocampa* processions had contact with humans driving, cycling or walking. The chance of human contact was higher in *T. pityocampa* compared to *O. lunifer*; possibly due to the number of people that attended the area, but most likely explained by the larvae being attracted to cleared areas of the forest (i.e. footpaths).

With this information, we can forewarn people to avoid infested areas especially in the morning or stay at least 80 m and 30 m away from host trees with *O. lunifer* and *T. pityocampa* nests respectively, during the pre-pupation procession period. If it is necessary to go to these high-risk areas, people should be visually

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

alert where they are walking or cycling and wear appropriate protective clothing and eyewear. Awareness is important for prevention, because these urticating caterpillars will disperse from the host tree to pupation sites every year.

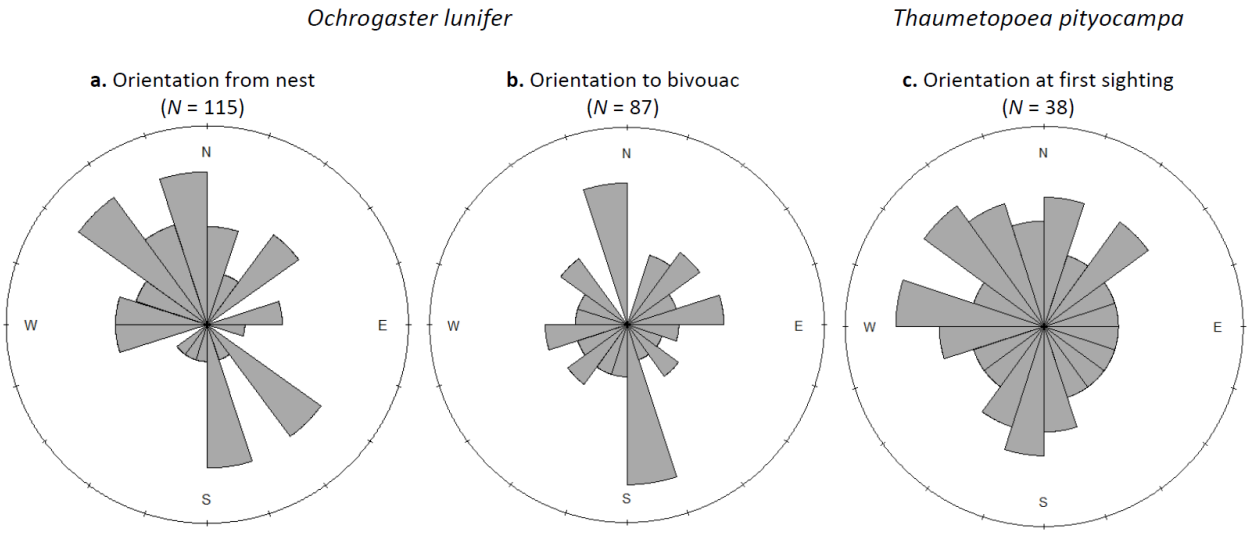


Figure 1. Rose diagrams of the orientation of pre-pupation processions of O. lunifer leaving the nest (a) and final orientation to the bivouac following the last turn of the leader (b), and of *T. pityocampa* at first sighting (c).

2. Result 2: Spatial orientation of social caterpillars is influenced by polarized light

Published as: Uemura M., Meglič A, Zalucki MP, Battisti A, Belušič G. 2021 Spatial orientation of social caterpillars is influenced by polarized light. Biol. Lett. 17: 20200736. https://doi.org/10.1098/rsbl.2020.0736

Methods

Through our observational experiments on pre-pupation processions of both species, it was feasible that like many other insects, both *O. lunifer* and *T. pityocampa* use polarised light for orientation cues. To demonstrate this, we conducted a manipulative experiment using polarizing filters (PF) above the leader of processions or single larvae (singletons). The experiments were first conducted on first instar (L1) *T. pityocampa* larvae in an outdoor setting at Tregnago, Veneto, Italy (45°51' N, 11°17' E). A sheet of 50 cm^2 white paper was used as the experimental arena where 10 first instars at a time were released in the middle of the sheet and behavioural observations were made. Four treatments were applied to the procession leader/singleton in the experiment for two minutes each: PF held above the larva in one orientation (horizontal), PF rotated 90° (vertical), PF removed and neutral density filter (NDF). The NDF was used as a control for the experiment to test if the shadow created by the PF influenced larval orientation. The change/no change in procession orientation was recorded after 30 s of treatment application. Additionally, the same experiment was done in the field with final instar pre-pupation *O. lunifer* and *T. pityocampa* processions at UQ Gatton campus and Leiria, Portugal (39°31' N, 9°07' W), respectively.

Morphological analyses of larval stemmata through scanning electron microscopy (SEM), light microscopy (LM) and transmission electron microscopy (TEM) were conducted to identify the likely organ responsible for polarized light vision.

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

Results

Application of PF either 'horizontally' or 'vertically' resulted in a directional change of the leader and the rest of the procession by 58–103° (Fig. 2). Similarly, the application of PF and then the removal of PF resulted in an orientational change of 49 - 96° (Fig. 2). In comparison, the NDF caused a heading change of 18–32° therefore, had a minimal effect on the larva's orientation (Fig. 2). Our results support findings (Wellington, 1953, 1955; Doane and Leonard, 1975) that holometabolous larvae change their orientation of travel proportionally to the PF angle.

Larvae of both species have six stemmata on each side of the head (Fig. 3a). Stemmata II–VI appear shiny, while stemma I appears opaque (Fig. 3b). SEM revealed that 2/3 of the surface of stemma I pointing upwards is rugged and 1/3 pointing downwards is smooth (Fig. 3c), whereas stemmata II–VI are smooth all around (Fig. 3d). The rugged surface of stemma I is a diffuser and a spatial low-pass filter for incident light. A similar opaque optical structure has evolved in the DRA ommatidia of honeybees and locusts (Meyer and Labhart, 1981; Homberg and Paech, 2002). These structures enlarge visual fields, decrease acuity and are thought to reduce the visual clutter caused by clouds, thereby stabilizing skylight polarization vision (Meyer and Labhart, 1981). We hypothesized that stemma I could harbour photoreceptors optimized for polarization vision. Indeed, LM and TEM images showed a single-tiered, cushion-shaped light-sensitive structure (rhabdom), formed of two pairs of photoreceptors with orthogonal and aligned microvilli (Fig. 3 e, f). Other stemmata have flower-shaped rhabdoms, formed of more than 3 photoreceptors in the distal and proximal tier; their microvilli are neither aligned nor orthogonal (Fig. 3 g, h). The rhabdom in stemma I is similar to rhabdoms in DRA ommatidia of Noctuid and Crambid moths, while the rhabdoms in stemmata II–VI resemble the lobed rhabdoms in the main retina of adult moths (Meinecke, 1981; Belušič, Šporar and Meglič, 2017). The conspicuous dioptrical apparatus and rhabdom clearly indicate that stemma I is optimized for polarization vision, while other stemmata do not show such optimizations and are thus suitable for general vision, such as intensity or colour contrast detection.

We have demonstrated that stemma I in social caterpillars is anatomically similar to a single ommatidium in the DRA of adult moths. Although it is a non-imaging polarization detector that samples only a fraction of the skylight pattern, a pair of stemmata is still capable of assisting spatial orientation, similar to the specialized simple eyes in certain spiders (Dacke *et al.*, 1999). Larval locomotion was manipulated with a PF, which showed that polarization vision is one of the mechanisms that guided their social behaviour. Skylight polarization pattern enables pre-pupation processions to have a constant heading away from the nest to disperse further and to avoid drift, which could result in a loop.

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

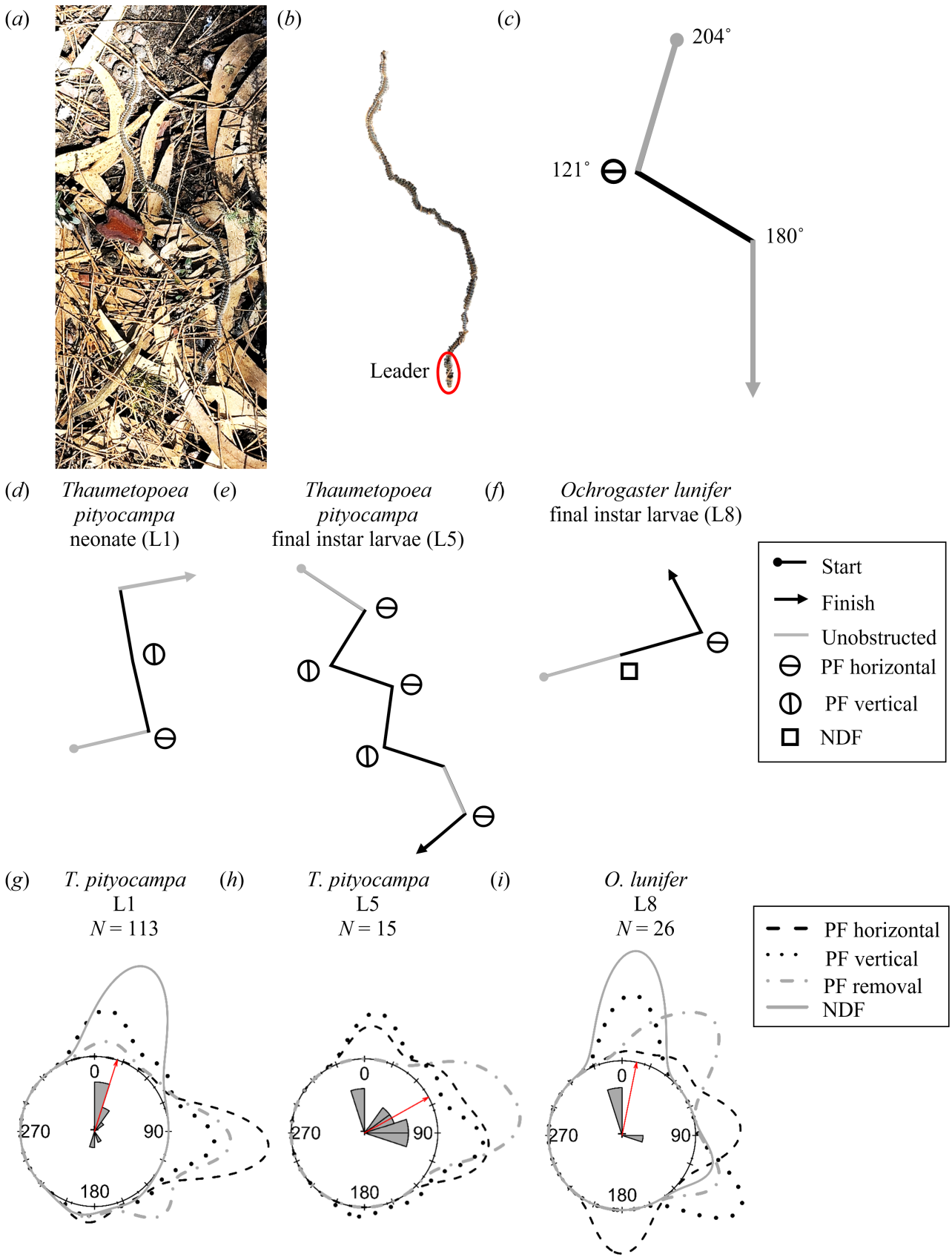


Figure 2. Influence of polarized light on caterpillar heading direction. (a) Final instar *T. pityocampa* pre-pupation procession after the experiment with/without a polarizing filter (PF). (b) Procession from (a) without background. (c) Schematic path from (b). Numbers indicate the orientation of the procession. (d–f) Schematic path of *T. pityocampa* L1, L5 and *O. lunifer* L8, respectively. (c–f) Each line segment represents

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

2 min duration of locomotion. (g–i) Circular plots with kernel density estimations (KDE) of summarized angular differences of *T. pityocampa* L1, L5 and *O. lunifer* L8 caused by PF and NDF. The KDE are represented as lines extruding in the outer circle. The rose histograms of (g,i) in the middle represent the angular difference after NDF application. In (h), NDF was unavailable, therefore data from PF horizontal was plotted. The red arrow represents the mean of the histogram data.

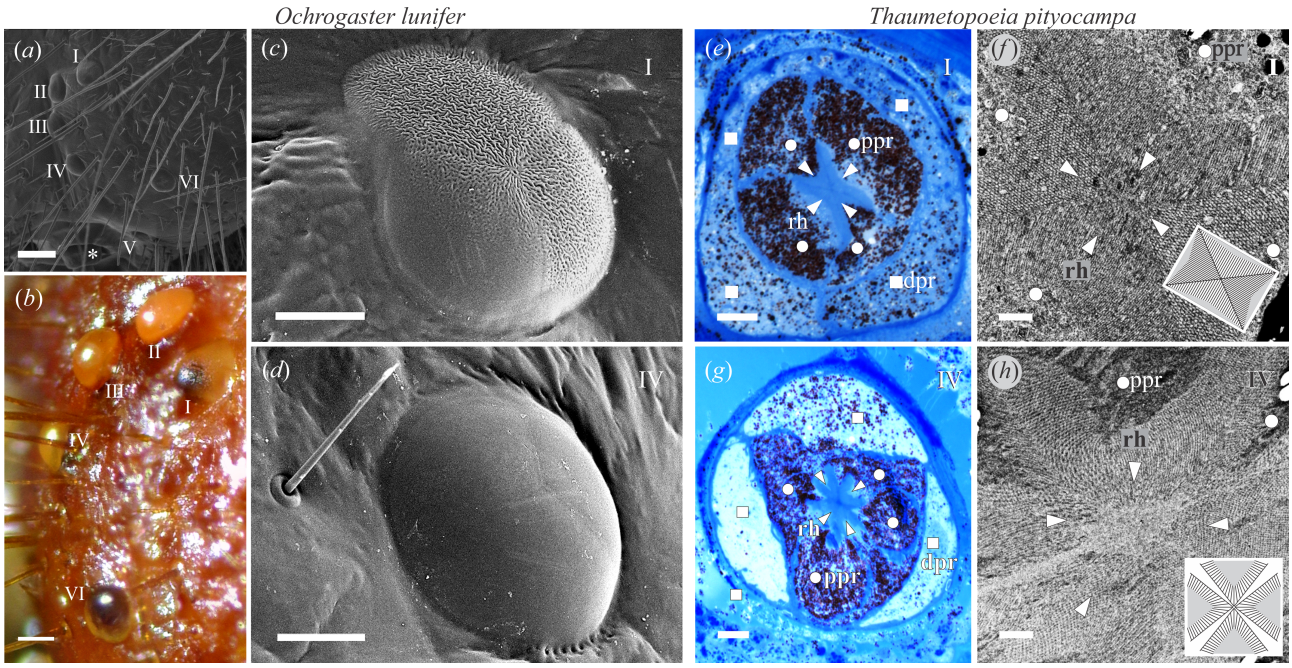


Figure 3. Anatomy of *O. lunifer* (a–d) and *T. pityocampa* (e–h) stemmata. (a,b) Side view of the left head capsule of final instar larva; (a) scanning electron micrograph (SEM); (b) stereomicrograph, stemma V hidden. Numbers refer to stemmata I–VI. (c,e,f) Stemma I; (c) SEM of the cornea; (e) light micrograph (LM) of the photoreceptors; (f) transmission electron micrograph (TEM) of the rhabdom. (d,g,h) Stemma IV; (d) SEM of the cornea; (g) LM of the photoreceptors; (h) TEM of the rhabdom. The bottom right corners in (f) and (h) are schematic diagrams of the rhabdom illustrating the microvillar orientation. In (a), the antenna is indicated by an asterisk; in (e,f,g,h), rhabdomeres (rh) are indicated by triangles, proximal photoreceptor bodies (ppr) by circles and distal photoreceptor bodies (dpr) by squares. Scale bars: (a) 200 µm; (b) 100 µm; (c,d) 50 µm; (e,g) 10 µm; (f,h) 1 µm.

3. Result 3: Behavioural plasticity and tree architecture shapes tent and foraging locations of pine processionary larval colonies

Published as: Uemura M., Zalucki M.P., Battisti A. 2021. Behavioural plasticity and tree architecture shape tent and foraging locations of pine processionary larval colonies. Entomologia Generalis 41: 121-136. DOI: 10.1127/entomologia/2020/1091

Methods

Lepidopteran females are generally selective when choosing oviposition sites to ensure the best survival for their offspring. Unlike most social and shelter building Lepidoptera, *Thaumetopoea pityocampa* eggs are oviposited randomly on the host tree (Tiberi 1983; Zamoum et al. 2015). *Thaumetopoea pityocampa* is gregarious throughout all larval instars and live in silken tents, spun repeatedly, and maintained by the

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

colony during larval development. In this study, we wanted to investigate if the initial egg orientation on the host tree affects the survival of the colony.

From the end of August through to September 2018, 88 *T. pityocampa* egg batches with pine needles attached were collected from Austrian pine *Pinus nigra* at Precastio. A single *T. pityocampa* egg batch was then transplanted on a *P. nigra* host tree free from natural egg batches in one of four compass orientations: north, east, south or west. Each colony was monitored once every one to three days up to the third instar (Sept-Oct) and then weekly to fortnightly thereafter until March 2019 when the larvae left the trees to pupate in soil. At each monitoring, the survival/viability, condition, and location of the colony on the tree were recorded.

Results

Survival of *T. pityocampa* colonies until final instar (L5) was not affected by egg batch orientation. However, the total number of eggs hatched had a marginal effect on the survival, i.e. colonies with more hatched eggs were more likely to survive until L5 than colonies with less hatched eggs. Increase in group size has been shown to increase larval survival by cooperative defence strategies and by dilution effects (McClure and Despland, 2011; Santana, Rodrigues and Zucoloto, 2017). In winter, it may be particularly important for *T. pityocampa* as more individuals enables the colony to spin more silk for better insulation (Breuer *et al.*, 1989) and to maintain a well-protected tent from avian predators.

Colonies that survived until L5, made an average of 4 tents (Fig. 4). After hatching, all colonies build their first tent beside or in very close proximity to the egg batch which is almost always on the current-year shoot. After the first tent, the colonies abandoned and built a new tent usually on a different branch and finally build a 'winter tent' in autumn as late instar larvae (Fig. 4). Younger and older *T. pityocampa* larval colonies established their tents in a southerly orientation on *P. nigra* trees (Fig. 5). Irrespective of different egg batch orientations, there was no significant difference in survival because *T. pityocampa* larvae are behavioural thermoregulators; and their movement on the tree correlates closely with the position of the sun. The study can affirm that younger *T. pityocampa* make several tents as a patch-restricted forager (i.e., larvae feed in the vicinity of the tent) and become central-place foragers (i.e., larvae move away from the tent as long as food is consumed) living in a permanent tent as they reach older instars (Fabre, 1898; Balfour-Browne, 1925; Fitzgerald and Costa, 1999). Explanations for this transition from patch-restricted forager to central-place forager may be the different natural enemies/mortality factors, plant defences and/or weather that *T. pityocampa* colonies encounter throughout different larval instars. When younger *T. pityocampa* larvae are developing, invertebrate predators are also active during these warm temperatures therefore, having a tent nearby is possibly a quick way of getting protection.

This study is the first to investigate detailed movements of all *T. pityocampa* larval instars at tree and branch scale. Current pest management practices for this species is aerial application of an entomopathogenic bacterium (*Bacillus thuringiensis kurstaki*) on infested host trees (Roques *et al.*, 2015). Younger caterpillars are more susceptible than older caterpillars (Battisti *et al.*, 1998) therefore, application of bacterial toxin will be more effective when they are younger. However, when *T. pityocampa* are younger instars, there are many non-target species that are active in summer through to autumn. New technologies such as drones (unmanned aerial vehicles) could assist with precise bacterial toxin application on L1 colonies and knowledge about where tents are constructed is helpful to limit consequences on non-target species.

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

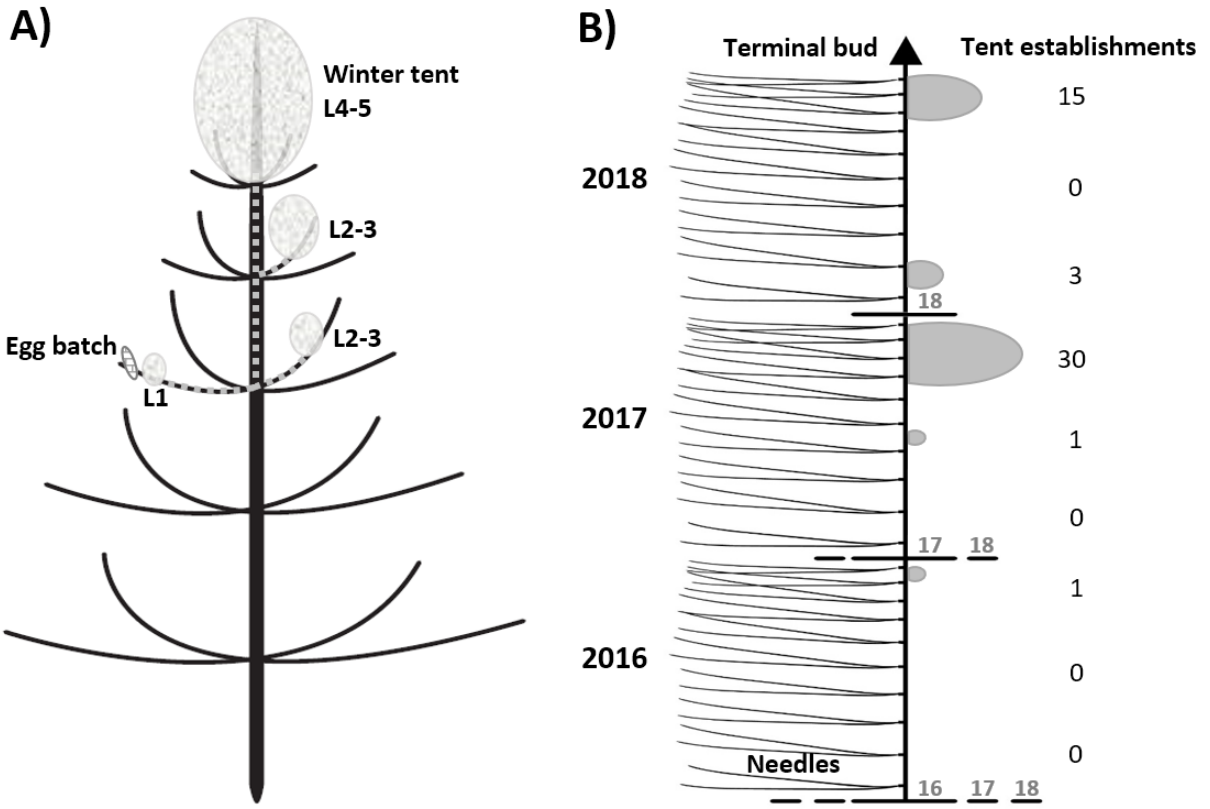


Figure 4. A) Schematic diagram of *T. pityocampa* colony movements and tent establishments (light grey ovals) on *P. nigra*. Dashed grey line represents the movements between abandoned and new tents, starting from the tent near the egg batch to the final winter tent at the most apical part of the tree. Size of tents get progressively larger through larval age. **B)** Schematic diagram of a *P. nigra* branch divided by dashed horizontal lines which represent the three years of growth (long shoots) going vertically and horizontally. The numbers 16, 17 and 18 in grey represent 2016, 2017 and 2018 (current-year of the study) shoots, respectively. The triangle at the end of the 2018 shoot represents the terminal bud. The semicircles on the right of the pine needles are the total number of tents that were built on that shoot position (basal, middle or apical) and year by younger instar (L1–2) *T. pityocampa* larvae. Diagrams not drawn to scale, drawn by Paolo Paolucci.

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

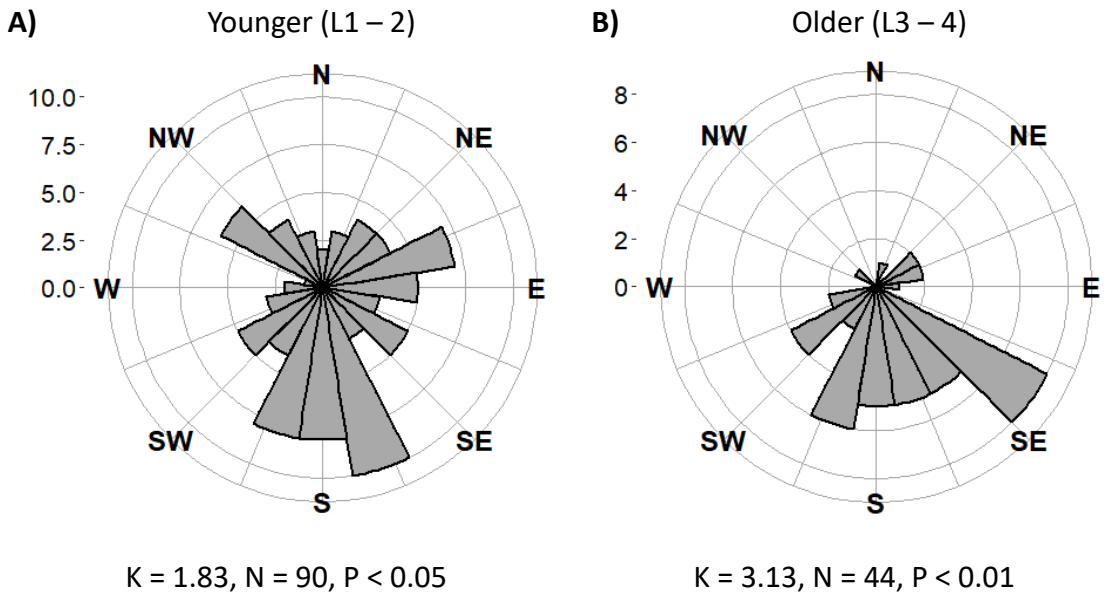


Figure 5. Distribution and frequency of where and how many A) younger (L1–2) and B) older (L3–4) *T. pityocampa* larvae built a tent on the host tree irrespective of transplanted egg batch orientation. The numbers on the left of each diagram correspond to the rings inside the circle and it represents the frequency of movements by larval colonies; starting from the smallest number in the centre to the largest number in the second last outer ring. Number in the centre represents the number of tents that were built at the most apical part of the tree canopy (leader shoot) which had no orientation. K and N represents the Kuiper's test statistic and number of colonies, respectively.

4. Conclusions

The following points summarize the main results of the work carried out with the processionary caterpillars and open the way to the exploitation of the results for a better management and control of the populations.

- The initial colonies of the larvae of the pine processionary moth are distributed homogenously in the tree canopy but tend to converge to the south-facing side of the tree as they moult to the second and third instar. The tendency becomes stronger in the fourth instar, when the final winter tent is built. This knowledge is important for i) the detection of the colonies, for example when an automatic image analysis is used for a rapid census of the population density; ii) for the application of a biopesticide (e.g. toxin of *Bacillus thuringiensis*) that can be restricted to the tent and surrounding feeding area.
- The larvae of all processionary moths use a solar compass to find a direction when moving on the tree and on the ground. The compass is based on the detection of polarised light and the mechanism is based on a special eye (stemma) located on both sides of the upper part of the head. This knowledge is important for i) predicting the direction taken by the larvae on the ground, which is essential to deploy measures addressed to avoid contact with humans and animals that can inadvertently get in contact with them; ii) developing devices addressed to interfere with the movement of the larvae to the locations offering the best performance.
- The larvae of all processionary moths can move on the ground for a considerable distance before finding a suitable pupation site. The pupation sites are thus distinctly located at some distance of the trees where the larvae fed. These results have two implications: i) the control of the larvae/ prepupae/pupae with natural enemies (e.g. entomopathogenic fungi) can be improved by a better

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

localization of the applications; ii) the area where urticating setae are dispersed during the procession and at the pupation sites can be better defined and measures taken to avoid an overlapping with the activity of humans and animals.

- The social behaviour and labour division among groups of individual larvae in the colony was first discovered in this project and may have a number of implications that are still on the way to be developed. For example, i) natural enemies activity, especially parasitoids and predators, could be manipulated in order to achieve the best biocontrol of the populations; ii) the silk production and the construction of the tent could be manipulated by the disruption of the orientation mechanisms of the larvae at the time of tent building.

All the results of the study offer a number of opportunities for a better management that ideally integrate different biological and behavioural methods in a systems approach to pest management. The inclusion of VOCs as an additional factor in regulating the behaviour of the larvae may provide further hints and we will hopefully achieve some results by the end of the project. The model of the processionary moth can be taken as an example for other insect herbivores that may negatively affect forest ecosystems and landscape trees. The innovative methods would prompt the natural regulation of the populations and limit the application of biopesticides to the target microsites.

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

Literature

Alonso, C. (1997) 'Choosing a place to grow. Importance of within-plant abiotic microenvironment for *Yponomeuta mahalebella*', Entomologia Experimentalis et Applicata, 83(2), pp. 171–180. doi: 10.1023/A:1002908817924.

Balfour-Browne, F. (1925) 'The evolution of social life among caterpillars', in Jordan, K. and Horn, W. (eds) The Proceedings of the Third International Congress on Entomology. Zurich, pp. 334–339.

Battisti, A. et al. (1998) 'Results and perspectives in the use of *Bacillus thuringiensis* Berl. var. kurstaki and other pathogens against *Thaumetopoea pityocampa* (Den. et Schiff.) in Italy (Lep., Thaumetopoeidae)', Journal of Pesticide Science, 71, pp. 72–76.

Belušič, G., Šporar, K. and Meglič, A. (2017) 'Extreme polarisation sensitivity in the retina of the corn borer moth *Ostrinia*', Journal of Experimental Biology, 220(11), pp. 2047–2056. doi: 10.1242/jeb.153718.

Breuer, M. et al. (1989) 'Studies on the exposition and temperature of nests of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Thaumetopoeidae) in Greece', Journal of Applied Entomology, 107(1–5), pp. 370–375. doi: 10.1111/j.1439-0418.1989.tb00271.x.

Cawdell-Smith, A. J. et al. (2012) 'Equine amnionitis and fetal loss: Mare abortion following experimental exposure to Processionary caterpillars (*Ochrogaster lunifer*)', Equine Veterinary Journal, 44(3), pp. 282–288. doi: 10.1111/j.2042-3306.2011.00424.x.

Dacke, M. et al. (1999) 'Built-in polarizers form part of a compass organ in spiders', Nature, 401(6752), pp. 470–473. doi: 10.1038/46773.

Dent, D. (2000) Insect pest management. CABI Pub.

Doane, C. C. and Leonard, D. E. (1975) 'Orientation and dispersal of late-stage larvae of *Porthetria dispar* (Lepidoptera: Lymantriidae)', The Canadian Entomologist, 107(12), pp. 1333–1338. doi: 10.4039/Ent1071333-12.

Dulaurent, A. M., Porté, A. J., van Halder, I., Vetillard, F., Menassieu, P., & Jactel, H. (2011). A case of habitat complementation in forest pests: Pine processionary moth pupae survive better in open areas. Forest Ecology and Management, 261(6), 1069-1076.

Fabre, J. (1898) 'Souvenirs Entomologiques', Sér, 6, pp. 298–392.

Fitzgerald, T. . and Willer, D. E. (1983) 'Tent-Building Behavior of the Eastern Tent Caterpillar *Malacosoma americanum* (Lepidoptera: Lasiocampidae)', Journal of the Kansas Entomological Society, 56(1), pp. 20–31.

Fitzgerald, T. and Costa, J. (1999) 'Collective behavior in social caterpillars', in Detrain, C., Deneubourg, J. L., and Pasteels, J. M. (eds) Information Processing in Social Insects. Basel: Birkhäuser, pp. 379–400. doi: https://doi.org/10.1007/978-3-0348-8739-7_20.

Floater, G. J. and Zalucki, M. P. (1999) 'Life tables of the processionary caterpillar *Ochrogoster lunifer* Herrich-Schäffer (Lepidoptera:Thaumetopoeidae) at local and regional scales', Australian Journal of Entomology, 38(4), pp. 330–339. doi: 10.1046/j.1440-6055.1999.00122.x.

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

Homberg, U. and Paech, A. (2002) 'Ultrastructure and orientation of ommatidia in the dorsal rim area of the locust compound eye', Arthropod Structure and Development, 30(4), pp. 271–280. doi: 10.1016/S1467-8039(02)00010-5.

Jactel, H. et al. (2015) 'Insect – Tree Interactions in *Thaumetopoea pityocampa*', in Roques, A. (ed.) Processionary Moths and Climate Change: An Update. Dordrecht-Versailles: Springer-Quae, pp. 265–310.

McClure, M. and Despland, E. (2011) 'Defensive responses by a social caterpillar are tailored to different predators and change with larval instar and group size', Naturwissenschaften, 98(5), pp. 425–434. doi: 10.1007/s00114-011-0788-x.

Meinecke, C. C. (1981) 'The fine structure of the compound eye of the African armyworm moth, *Spodoptera exempta* Walk. (Lepidoptera, Noctuidae)', Cell and Tissue Research. Springer-Verlag, 216(2), pp. 333–347. doi: 10.1007/BF00233623.

Meyer, E. P. and Labhart, T. (1981) 'Pore canals in the cornea of a functionally specialized area of the honey bee's compound eye', Cell and Tissue Research, 216(3), pp. 491–501. doi: 10.1007/BF00238646.

Moore, L. V et al. (1988) 'Western tent caterpillars prefer the sunny side of the tree, but why?', Oikos, 51(3), pp. 321–326.

Mullen, G. R. and Durden, L. A. (2009) 'Moths and butterflies (Lepidoptera)', in Mullen, G. and Durden, L. A. (eds) Medical and Veterinary Entomology. 2nd edn. Boston: Academic Press, pp. 353–368.

Perkins, L. E. et al. (2016) 'The urticating setae of *Ochrogaster lunifer*, an Australian processionary caterpillar of veterinary importance', Medical and Veterinary Entomology, 30(2), pp. 241–245. doi: 10.1111/mve.12156.

Robredo, F. (1963) 'Las procesiones de crisalidacion de *Thaumetopoea pityocampa* Schiff.', Boletín de Plagas Forestales, 6, pp. 122–130.

Roques, A. et al. (2015) 'Climate warming and past and present distribution of the processionary moths (*Thaumetopoea* spp.) in Europe, Asia Minor and North Africa', in Processionary Moths and Climate Change: An Update, pp. 81–162.

Ruf, C., Freese, A. and Fiedler, K. (2003) 'Larval sociality in three species of central-place foraging lappet moths (Lepidoptera: Lasiocampidae): A comparative survey', Zoologischer Anzeiger, 242, pp. 209–222.

Santana, A. F. K., Rodrigues, D. and Zucoloto, F. S. (2017) 'Larval aggregation in a Neotropical butterfly: risky behaviors, per capita risk, and larval responses in *Ascia monuste orseis*', Behavioral Ecology and Sociobiology. Behavioral Ecology and Sociobiology, 71(12), p. 174. doi: 10.1007/s00265-017-2403-4.

Steinbauer, M. J. (2018) 'Wing pattern polyphenism in two behavioural forms of *Ochrogaster lunifer* (Lepidoptera: Notodontidae)', Austral Entomology, 58(2), pp. 432–442. doi: 10.1111/aen.12329.

Tiberi, R. (1983). Sulla distribuzione delle ovature di *Thaumetopoea pityocampa* (Den. & Schiff.) in un giovane impianto di *Pinus pinaster* e *P. insignis*. Redia (Firenze), 66, 603–614.

Uemura, M. et al. (2021) 'Spatial orientation of social caterpillars is influenced by polarized light', Biology letters, 17, p. 20200736.

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271

Uemura, M., Zalucki, M. P. and Battisti, A. (2020) 'Behavioural plasticity and tree architecture shapes tent and foraging locations of pine processionary larval colonies', Entomologia Generalis.

Wellington, W. G. (1953) 'Motor responses evoked by the dorsal ocelli of *Sarcophaga aldrichi* Parker, and the orientation of the fly to plane polarized light', Nature, 172, pp. 1177–1179.

Wellington, W. G. (1955) 'Solar heat and plane polarized light versus the light compass reaction in the orientation of insects on the ground', Annals of the Entomological Society of America, 48(1–2), pp. 67–76. doi: 10.1093/aesa/48.1-2.67.

Zamoum, M., Martin, J.-C. and Bensidi, A. (2015) 'Fecundity of the pine processionary moth *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae) at the southern edge of its distribution range', Biologia, 70(3), pp. 386–392. doi: 10.1515/biolog-2015-0036.

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°771271