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RESEARCH ARTICLE

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Life in the lab: unlocking the biology and laboratory rearing of the litchi moth, *Cryptophlebia peltastica* (Meyrick) (1921)

Tamryn Marsberg[1]*, Sean D. Moore[1,2] and Martin P. Hill[2]

[1]*Citrus Research International, Port Elizabeth, South Africa.*
[2]*Centre for Biological Control, Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa.*

Cryptophlebia peltastica (Meyrick) (1921) (Lepidoptera: Tortricidae) is an agricultural and economically important pest of litchis and macadamias in South Africa. Non-chemical based control options for *C. peltastica* are required to reduce the economic importance of the pest. Understanding the biology of *C. peltastica* and effectively rearing this pest in the laboratory will facilitate the search for alternative control options. We adapted the *Thaumatotibia leucotreta* rearing protocol to successfully rear *C. peltastica* in the laboratory for the first time, allowing us to determine aspects of its biology. Females oviposited an average of 180.58 eggs per day, with a maximum of 506 eggs oviposited over their lifespan. Egg viability was 90.56 %. Five larval instars were determined using head capsule width measurement. The biology of *C. peltastica* was similar to that of *T. leucotreta*, also in the Grapholitini tribe of tortricids. This study is the first to report successful laboratory rearing and biological parameters of *C. peltastica*, the results of which have already proven to be useful in the discovery of a novel virus, which has been developed into a biopesticide and development of a postharvest cold disinfestation treatment.

CORRESPONDENCE
Tamryn Marsberg

EMAIL
tammy@cri.co.za

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INTRODUCTION

Litchi chinensis (Sonnerat) (Sapindales: Sapindaceae), also known as litchi or lychee, is a medium to large, evergreen tree that bears litchi fruit (Storey 1973; Hieke et al. 2002). Litchi is native to the southern subtropics of China and is now a commercially grown crop in various subtropical countries, such as Asia, Australia, India, Thailand, Taiwan, Reunion Island, Vietnam, Hawaii and South Africa. Litchis are considered a delicacy and hence an important agricultural crop (Menzel 1985; Piper 1988; Jacobi et al. 1993; Batten et al. 1994; Jiang & Chen 1995; Huang et al. 2005). Litchi cultivation in South Africa was first recorded in KwaZulu-Natal province in 1876, when trees were imported from Mauritius. Litchis are now produced in the KwaZulu-Natal, Mpumalanga and Limpopo provinces (Department of Agriculture, Forestry and Fisheries 2011, 2013; Subtrop 2022; Subtrop 2024).

Litchi trees are known to be irregular bearers, due to several factors, including poor pollination, failure to flower, poor fruit development, early fruit drop and various pests, which could all be due to suboptimal climatic conditions (Menzel 1983, 1984). Due to the irregular bearing of litchi trees, the litchi industry has not yet reached the commercial status of various other horticultural crops produced in South Africa. However, with the establishment of the South African Litchi Growers Association (SALGA) in 1987, the total gross value of litchis has increased. During the 2016/17 season, litchis contributed 6.5 % (R264 million) of the gross value of subtropical crops produced in South Africa. In the 2022/23 season, 9 335 tons of litchis were produced, of which 5 086 tons were exported (DALRRD 2020; SALGA production stats 2023).

Production of litchis in South Africa is mainly affected by climatic factors and the presence of an economically important pest, *Cryptophlebia peltastica* (Meyrick) (1921) (Lepidoptera: Tortricidae), commonly referred to as litchi moth. *Cryptophlebia peltastica* is a polyphagous agricultural pest of litchis and macadamias in South Africa, Mauritius, Seychelles, Réunion and Madagascar. Other hosts include *Delonix regia* (Hook), *Tamarindus indica* (Linnaeus), *Bauhinia* spp. (Linnaeus), *Caesalpinia pulcherrima* (Linnaeus), *Acacia* spp. (Linnaeus) and *Cassia* spp. (Linnaeus) (Waite & Hwang, 2002; Manrakhan et al. 2008). In South Africa, *C. peltastica* can cause significant pre- and post-harvest losses to litchi crops, potentially reducing annual yields within the industry (Schoeman et al. 2004; Grové & de Beer 2005). *Cryptophlebia peltastica* is considered a phytosanitary pest in certain export markets and thus, maintaining control over this pest is essential to ensure continued market access (de Villiers 1992; Booysen et al. 2006; Schoeman et al. 2009).

Control strategies for *C. peltastica* must adhere to Good Agricultural Practices (GAP) standards to ensure compliance with export regulations (Grové 2022). Effective pest management requires a comprehensive approach encompassing prevention, monitoring, and intervention. Current control methods for *C. peltastica* include the use of parapheromones for adult monitoring, fruit bagging, and biological control agents, such as the egg parasitoid *Trichogrammatoidea cryptophlebiae* (Nagaraja, 1979) (Hymenoptera: Trichogrammatidae). Additionally, the mating disruption product, X-Mate™ LFM (Insect Science) is registered for adult population suppression (de Villiers 1992; Booysen et al. 2006; Schoeman et al. 2009; Grové 2022; Subtrop 2024).

Consequently, control options for *C. peltastica* are limited, thus there is a need for the development of additional strategies, particularly biological pesticides. The successful development and testing of such alternatives require a laboratory-reared culture of *C. peltastica*,

which serves as a critical foundation for research and the formulation of environmentally sustainable pest management solutions (Shapiro 1992). However, challenges in rearing a laboratory culture have been attributed to the limited literature on the biology of *C. peltastica* (Timm 2005).

Attempts to rear *C. peltastica* under laboratory conditions have largely been unsuccessful, due to challenges related to mating and oviposition (Steyn & Schoeman 2007). Hepburn et al. (2009) successfully established a *C. peltastica* culture, using a protocol similar to that employed for *Thaumatotibia leucotreta* (Meyrick) (Lepidoptera: Tortricidae). However, due to the insufficient number of larvae collected, a mass-reared culture could not be sustained beyond a few generations. These findings highlighted the need for further research into optimizing rearing techniques, which would facilitate the advancement of alternative control measures for *C. peltastica*.

Prior to our study, no culture of litchi moth was reported to have been successfully maintained under laboratory conditions for more than a few generations and thus limited research on the biology and life history of *C. peltastica* has been possible. This study aimed to develop a successful rearing protocol for maintaining *C. peltastica* under laboratory conditions, using information adapted from Steyn and Schoeman (2007) and Hepburn et al. (2009). Establishing a successful protocol will enable further investigation into the biology of *C. peltastica*, and has already facilitated the identification and production of a baculovirus as a biopesticide, has supported cold disinfestation trials that can contribute to the development of a postharvest cold disinfestation treatment (Moore et al. 2018) and enables production of an egg parasitoid (Stirk 2025; Stirk et al. 2026).

MATERIALS AND METHODS

Cryptophlebia peltastica was initially obtained as larvae from infested macadamia nuts and from *C. pulcherrima* (pride of Barbados) pods that were collected between 2008 and 2011, from Mbombela (25.466° S, 30.985° E) (Mpumalanga, South Africa). Larvae were reared under laboratory conditions at Rhodes University (Makhanda, Eastern Cape, South Africa). The culture was subsequently shared with River Bioscience (Pty) Ltd (Addo, Eastern Cape) for continued rearing. The rearing protocol for *C. peltastica* was adapted from the methods used by Ripley et al. (1939), Theron (1948), Schwartz (1971) and Moore (2002) for *T. leucotreta*. *Cryptophlebia peltastica* was reared in a controlled environment (CE) room at 27 ± 1°C, relative humidity of 60–80% and photoperiod of 16:8 (light to dark). Developmental trials were also conducted under these conditions. Adult moths were held in oviposition cages consisting of an inverted metal sieve (30 cm diameter), placed over a sheet of wax paper. The wax paper provided a suitable oviposition substrate for the female moths. Cotton wool, moistened with 10% sugar solution in distilled water, was placed inside the cage as an adult food source. Egg sheets were collected every second day and divided into segments of approximately 300 eggs. These segments were surface sterilised by dipping them for 2–3 s in a 6% formaldehyde solution. Egg sheets were then placed into glass jars (325 ml Consol honey jars), containing 50 g of *T. leucotreta* artificial diet (dry mix) (Moore et al. 2014) and 50 ml distilled water. The jars were then sealed with breathable membrane fabric (PTEE 2203, BreathTech, South Africa) lids. Jars containing the artificial diet mixture were then cooked and sterilised by autoclaving for 18 min at 121 °C, jars were allowed to cool before eggs were introduced. The egg sheets were suspended from the lid of the jar, to reduce the possibility of fungal contamination of the artificial diet, i.e. direct transfer of any surviving fungal spores from the egg sheet to the diet. Once pupal development was observed and the pupae had hardened, they were removed from the artificial diet and placed under an inverted sieve.

During rearing, various aspects of the biology of *C. peltastica* were determined. These included duration of the life cycle, fecundity and fertility of females, egg and larval development, number of larvae reared per jar, larval weight and larval yield per gram of diet. The number of larvae reared per jar was determined by counting the number of larvae per jar in each of 35 larval jars from the laboratory-reared culture. This was replicated three times. For larval weight, 10 jars containing fifth instar larvae were selected from the laboratory culture. Thirty larvae were randomly selected from each of the 10 jars and weighed. This was replicated three times. From these results, the larval yield per gram of diet was calculated. To determine larval yield per gram of diet, the initial quantity of diet added to each jar was recorded prior to inoculation. At the completion of larval development, the remaining diet and frass were removed, and the jars reweighed to estimate diet utilisation. Control jars containing diet, but no larvae, were maintained under the same environmental conditions to account for moisture loss from the diet over time. Larval yield per gram of diet was subsequently calculated using the corrected diet consumption values and the total larval biomass produced per jar.

Fecundity was recorded by placing a single pair (one male and one female) of moths, which eclosed on the same day, under an inverted sieve (9 mm diameter), positioned over a sheet of wax paper. Cotton wool moistened with 10% sugar water was placed inside the cage. Oviposition was then recorded by removing the wax paper every 12 h and replacing it with a clean sheet. The number of eggs was counted and recorded. Eggs oviposited on the sieve were recorded at the end of the trial. This process continued until the female died and was replicated with 12 moth pairs.

Egg development was recorded by placing a clean wax sheet under an inverted sieve containing approximately 30 females and males. After 12 h, the sheet was removed. Egg sheets were divided into 10 samples, with each sample containing 30 eggs. Egg development was recorded every 12 h, by taking a picture under a dissecting microscope and recording how long the eggs took to develop and hatch. This was replicated three times.

The percentage egg hatch was determined by placing a clean wax sheet under a sieve containing approximately 30 females and males. After 12 h, the sheet was removed. The eggs were then inspected using a Leica (Switzerland) EZ4D microscope to determine whether eggs were clumped or singly oviposited. Egg sheets with an even distribution of singly oviposited eggs were used, as the mortality of clumped eggs could be higher (Moore 2002). These eggs were divided into six samples, with each sample containing 30 eggs. The egg sheets were left for 5 d and then viewed under a dissecting microscope (Leica (Switzerland) EZ4D microscope) to determine the number and, hence, proportion of hatched eggs. This was replicated three times.

Larval development was recorded by placing a clean wax sheet under a sieve containing approximately 30 females and males. The wax sheet was left for 12 h and then removed. The egg sheet was divided into 95 sections, each containing 30–40 eggs each. One of these sections was placed into a petri dish, for observation for the first ±120 h to record neonate hatching and measuring of body length and head capsule width. A second section of eggs was placed into a petri dish containing a thin layer of artificial diet, which allowed for easy access to the larvae for measurements. This petri dish was inspected twice, at 12 h intervals. Each remaining egg sheet section was placed into a honey jar containing artificial diet, as previously described, totalling 90 honey jars. Twenty larvae were collected every 12 h from a single jar. The head capsule width and body length of each larva were measured using a dissecting microscope with a graduated scale on the ocular. Dyar's rule was then applied to determine a relationship between instar and head capsule width

(Dyar 1890):

$$\text{Dyar's ratio} = \frac{\frac{2\text{nd}}{1\text{st}} + \frac{3\text{rd}}{2\text{nd}} + \frac{4\text{th}}{3\text{rd}} + \frac{5\text{th}}{4\text{th}}\left(\text{instar mean head capsule width}\right)}{n\left(\text{number of larvae measured}\right)}$$

Pupal development was recorded by selecting a jar containing approximately 20 fifth instar larvae. The jar was inspected daily to record pupal duration, defined as the period from onset of pupation to adult eclosion. This was repeated three times.

The sex ratio was determined by randomly collecting several hundred pupae (n = 732). Pupae were sexed using the morphological difference recorded by Timm et al. (2007), where males were found to have two protrusions on their last abdominal segment, which were absent in females.

RESULTS

Laboratory cultures of *C. peltastica* were successfully established at Rhodes University and River Bioscience rearing cultures grew exponentially to a point where a constant high number of jars of larvae could be produced from each generation, with the possibility to further increase the size of the culture. The number of larvae counted per jar ranged from 15 to 224, with a mean of 87 ± 4.27 (mean ± SE) (n = 105) larvae per jar. The weight of the fifth instar larvae ranged from 62.2 to 153. 3 mg, with a mean weight of 100.56 ± 0.49 mg (n = 900). These values were then used to determine the larval yield per gram of diet, which was calculated at 0.194 larvae per gram of diet.

The number of eggs oviposited per female ranged from 10 to 506 eggs, with a mean of 180.58 ± 47.76 (n = 12). Eggs hatched 4 d after oviposition at 27 ± 1°C and 60–80% RH. During this period, egg development was marked by changes in the appearance of the egg, which differed noticeably after approximately every 12 h. Newly oviposited eggs were initially creamy coloured but later turned red, and 24 h prior to hatch, the black head capsule of the larva could be observed (Figure 1). The percentage egg hatch ranged from 80% to 97%, with a mean of 90.56 ± 1.22% (n = 540).

Larval development was recorded by measuring the head capsules and body lengths of the developing larvae. A geometrical progression graph was used to plot a straight line, determining the presence of five instars, based on Dyar's rule. Using Dyar's ratio, the mean increment in head capsule width between each instar was calculated to be 0.290 ± 0.066 mm (n = 20) (Dyar 1890; Hsia & Kao 1987).

Mean (± SE) head capsule widths (n = 20 head capsules measured at each interval) progressed through each instar (1^{st}–5^{th}) as follows: 0.39 ± 0.01 mm, 0.50 ± 0.00 mm, 0.85 ± 0.02 mm, 1.28 ± 0.04 mm and 1.53 ± 0.01 mm (Table 1). Neonates were 1.26 ± 0.03 mm in length with a black head capsule and a transparent to cream-coloured body. Second to third instar larvae retained the same appearance as neonates. Colour change was apparent in the fourth instar, where the head capsule changed to dark brown, and the body became pink from a black head capsule and cream coloured body. The fifth instar larvae had a darker pink appearance and a lighter brown head capsule with a mean body length of 17.24 ± 0.20 mm (Table 1; Figure 2). At 27 ± 1°C and 60–80% RH, larval development from egg hatch

Table 1: Head capsule width and body length measurements of the five instars of *Cryptophlebia peltastica*.

Instar	Head capsule width (mm)		Body length (mm) (mean ± SE)
	Range	Mean ± SE	
1st	0.3 – 0.5	0.39 ± 0.01	1.26 ± 0.03
2nd	0.5 – 0.7	0.50 ± 0.00	2.66 ± 0.11
3rd	0.7 – 1.2	0.85 ± 0.02	6.49 ± 0.22
4th	1.2 – 1.6	1.28 ± 0.04	11.59 ± 0.35
5th	1.5 – 1.8	1.53 ± 0.01	17.24 ± 0.20

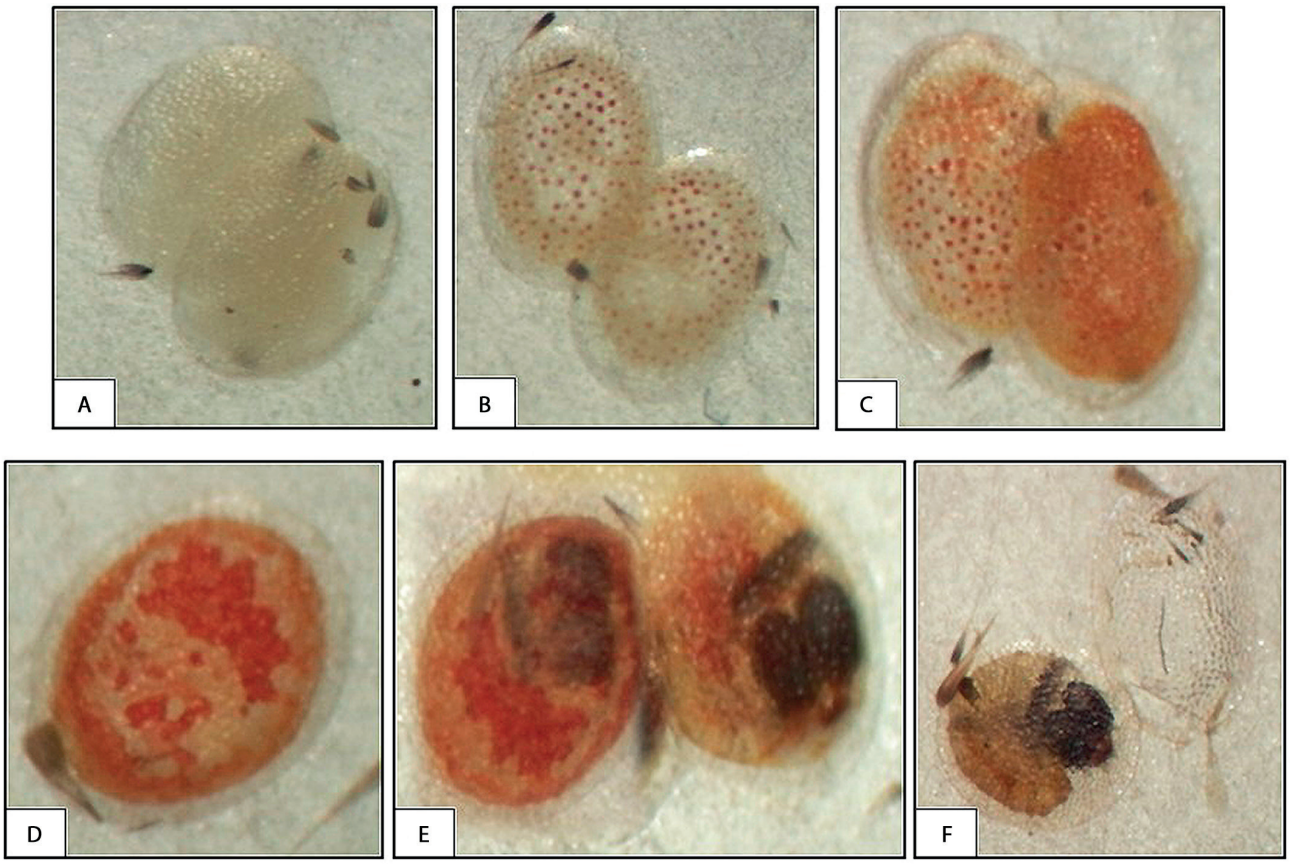

Figure 1: *Cryptophlebia peltastica* egg development (A: day 0, B: day 1, C: day 2, D: day 3, E: day 4 and F: day 5 (hatched and unhatched egg))

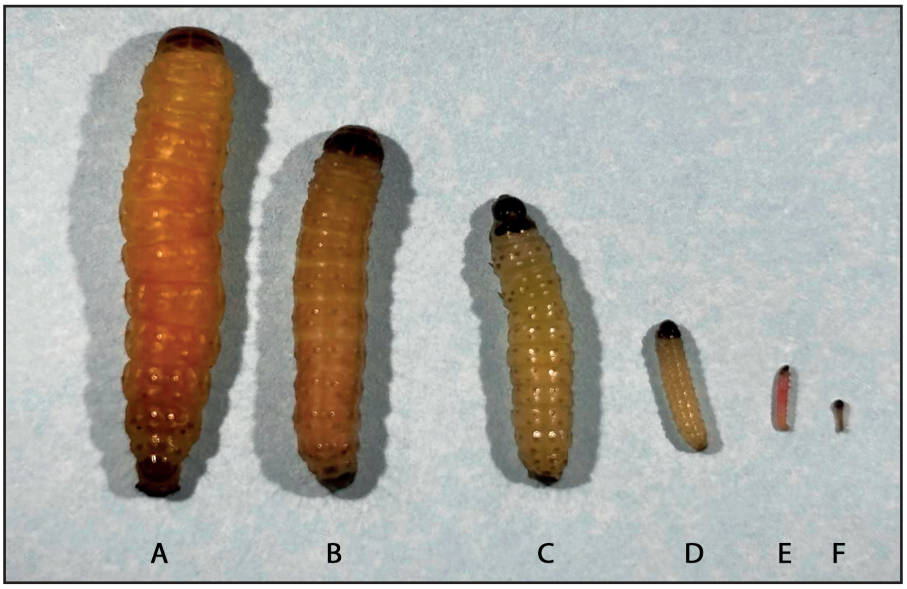

Figure 2: *Cryptophlebia peltastica* larval development from first to fifth instar (A: fifth instar, B: fourth instar, C: third instar, D: second instar, E: first instar, F: neonate).

to pupation was 19 d, with pupation lasting approximately 10 d before eclosion occurred. Under these conditions, the life cycle of *C. peltastica*, from egg to adult, took approximately 29 days.

The female to male sex ratio of pupae was 1.1:1. A chi-square test indicated no significant difference ($\chi^2 = 0.99$, $p < 0.05$, $n = 732$) between the number of male and female pupae.

DISCUSSION

This study reports the first detailed description of successful laboratory rearing of *C. peltastica*, providing thorough insights into its life history parameters and highlighting its biological similarities and distinctions relative to other *Grapholitini* tortricids, *T. leucotreta* and *Cydia pomonella* (Linnaeus) (1758) (Lepidoptera: Tortricidae). Establishing a laboratory culture of *C. peltastica* not only facilitates basic biological studies but also lays the foundation for the development of biological control tools and phytosanitary treatments essential for integrated pest management (IPM) in litchis and macadamias.

A key finding is that the fecundity of *C. peltastica* (average of 180 eggs per female) is lower than that reported for *T. leucotreta* (average of 500 eggs per female) (Moore 2004; Mkiga et al. 2019), but comparable to *C. pomonella* (average of 220 eggs per female) (Riedl et al. 1976; Howell 1991) (Table 2). This lower reproductive output suggests that *C. peltastica* may exert its pest status not through particularly high fecundity but through its polyphagy, cryptic larval feeding and ability to infest fruit late in development, thereby complicating control. Moreover, its high egg viability (average 90% hatch) ensures that even moderate oviposition rates might sustain damaging populations in orchards. However, hatch rate is expected to be much lower in the field due to an array of biotic and abiotic hurdles. Furthermore, successful fruit penetration may be diminished in a manner similar to that observed with *T. leucotreta* (Love et al. 2014).

Cryptophlebia peltastica has five instars, consistent with other tortricids (Daiber 1979; Chambers 2014; Kuyulu & Genç 2019). However, *C. peltastica* larvae reached greater body mass (average 100.56 mg at fifth instar) than *T. leucotreta* (average 38 mg) and *C. pomonella* average 50 mg). This larger size suggests higher consumption rates per larva and potentially more extensive fruit damage compared with *T. leucotreta*, despite fewer individuals per unit diet. This finding has ecological and applied implications; while *C. peltastica* may not achieve the same population densities under laboratory rearing, its individual larvae may pose a higher per capita risk to fruit quality in the field.

Table 2: Life history parameters of three economically important laboratory reared pest, *Cryptophlebia peltastica*, *Thaumatotibia leucotreta* (Blomefield & Giliomee 2009) and *Cydia pomonella* (Chambers 2014; Kuyulu & Genç 2019).

	C. peltastica	***T. leucotreta***	***C. pomonella***
Fecundity/female	180 eggs	500 eggs	222 eggs
Egg incubation time	4 days	3.5 days	4.2 days
Egg hatch	90.56%	91.80%	83.73%
Instars	5	5	5
Fifth instar head capsule width	1.53 mm	1.37 mm	1.55 mm
Fifth instar body length	17.24 mm	13.00 mm	14.00 mm
Fifth instar weight	100.56 mg	38.00 mg	49.86 mg

*All experiments were completed at ± 27˚C

Developmental timing was broadly similar among the three species, with complete life cycles of approximately 28–32 days under optimal laboratory conditions (25–27 °C, 60–80% RH). Notably, egg development in *C. peltastica* (average 4.0 d) closely parallels *T. leucotreta* (3.5 days) and is shorter than *C. pomonella* (average 4.2–5.0 d) under comparable conditions (Gilligan & Epstein 2014). These subtle differences in developmental rate are important for timing interventions such as egg parasitoid releases or mating disruption strategies, as even small variations can affect synchrony between pest and control agent.

Cultures of both *T. leucotreta* and *C. pomonella* have been successfully established in the laboratory and are widely used in research and commercial mass production of various control agents for use in pest control programmes. Laboratory rearing of insects comes with both challenges and advantages. Benefits of laboratory reared insects include repeatability of experiments due to controlled environmental conditions, reduced genetic variability, absence of environmental stressors and natural enemies, and large numbers of individuals always being available. However, challenges experienced with laboratory reared insects include artificial selection, genetic drift, differences in fecundity and life history traits, behavioural alterations and lack of natural microbiota (Grayson et al. 2015; Hoffmann & Ross 2018; Gloria-Soria et al. 2019). These challenges may affect how these insects perform, if needed for use in the field, such as in a sterile insect technique (SIT) programme, or how they

respond to certain control options (chemical or biological) relative to wild populations (Grayson et al. 2015; Hoffmann & Ross 2018; Gloria-Soria et al. 2019). To mitigate these challenges, field studies should be used to validate laboratory results, and wild individuals should be periodically added to the laboratory culture to introduce genetic diversity (Joslyn 1984).

The comparative analysis of life history traits among *C. peltastica*, *T. leucotreta* and *C. pomonella* underscores the importance of species-specific knowledge in IPM. The high fecundity of *T. leucotreta* and its capacity for continuous reproduction in tropical environments make it a more common pest under certain conditions, whereas *C. pomonella* has evolved as a temperate pest tightly linked to seasonal host availability. The life history traits of *C. peltastica* lies between these two extremes, with moderate fecundity but high larval biomass, suggesting that management programmes must account for both population growth potential and individual larval impact. Importantly, this study provided an opportunity to investigate whether control strategies used against *T. leucotreta*, such as baculoviruses and cold treatments, are also effective against *C. peltastica* (Marsberg et al. 2018; Moore et al. 2018), thereby reinforcing the value of cross-species approaches within Grapholitini.

Importantly, the establishment of a laboratory culture, enabled by this study, has led to several practical outcomes. First, it facilitated the isolation and characterisation of a novel alphabaculovirus, i.e. *Alphabaculovirus crypeltasticae* (CrpeNPV) (Marsberg et al. 2018). Molecular and morphological analyses confirmed the novelty of this virus and the high degree of pathogenicity not only against *C. peltastica*, but also the two closely related species *T. leucotreta* and *C. pomonella*. CrpeNPV is now mass-produced in laboratory-reared *C. peltastica* larvae and is commercially available from River Bioscience under the trade names CodlMax™ and MultiMax™. It is used for the biological control of *Cydia pomonella* in pome fruit, as well as *T. leucotreta*, *T. batrachopa* and *C. peltastica* in litchis and various nut crops (Marsberg et al. 2018).

Secondly, maintaining a laboratory culture of *C. peltastica* also allowed for the development of a postharvest cold treatment protocol for litchi exports. Since *C. peltastica* is considered a phytosanitary pest in certain export markets, the development of an effective postharvest treatment may be extremely useful. Moore et al. (2018) demonstrated that exposure to 1 °C for 13 days resulted in complete mortality, confirming the species high susceptibility to cold treatment. Importantly, their study also showed that any cold protocol effective against *T. leucotreta* would simultaneously control *C. peltastica*, since *T. leucotreta* exhibits greater cold tolerance and *C. peltastica* succumbs more rapidly under the same conditions. This is a particularly valuable finding, as both *T. leucotreta* and *C. peltastica* are recognised as pests of litchis, both with quarantine status for certain markets.

Furthermore, additional benefits of maintaining laboratory cultures include the potential for producing sterile insects for use in a Sterile Insect Technique (SIT) programme, which could provide a non-chemical suppression method for *C. peltastica* in the field, as demonstrated successfully for *T. leucotreta* (Hofmeyr et al. 2015; Moore 2021). Similarly, mass-reared *C. peltastica* eggs and larvae could serve as a reliable host source for the mass rearing of egg parasitoids such as *T. cryptophlebiae*, facilitating the biological control of *C. peltastica* (Stirk 2025; Stirk et al. 2026).

Therefore, the successful establishment and maintenance of a laboratory reared culture of *C. peltastica* has produced practical outcomes, including the discovery and commercialisation of CrpeNPV, a virus biopesticide now used against multiple tortricid pests in agricultural settings (Marsberg et al. 2018), and the development of a postharvest cold treatment, potentially supporting market access for South African litchis (Moore et al. 2018). These outcomes demonstrate how basic biological studies can translate directly into applied pest management solutions. Future work should aim to explore host–pathogen–insect interactions and assess the behavioural ecology of laboratory versus field populations to ensure robust transferability of laboratory findings to field applications.

CONCLUSION

Therefore, this successful establishment and maintenance of a laboratory culture of *C. peltastica* have already produced practical outcomes, enabling detailed insights into its life history parameters. The research highlights the biological similarities and distinctions of *C. peltastica* relative to other closely related tortricid pests such as *T. leucotreta* and *C. pomonella*. The establishment of a laboratory culture has facilitated applied research outcomes, including the discovery of a novel alphabaculovirus (CrpeNPV) and the development of a postharvest cold treatment for litchi exports. Although these outcomes have already been published, the rearing method and successful culture establishment described here preceded and, thus, enabled these breakthroughs. These achievements underscore the importance of laboratory-based biological research for advancing integrated pest management strategies and maintaining phytosanitary standards for export crops.

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COMPETING INTERESTS

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTIONS

TM conceived and designed the study, conducted the experiments, and drafted the manuscript. SDM provided supervision, contributed to data interpretation, and manuscript revisions. MPH supervised the project, provided conceptual input, and critically reviewed the final version of the manuscript. All authors read and approved the final manuscript.

ORCIDS

Tamryn Marsberg: https://orcid.org/0000-0001-9444-7484
Sean D. Moore: https://orcid.org/0000-0002-4155-4187
Martin P. Hill: https://orcid.org/0000-0003-0579-5298

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