HARPER ADAMS UNIVERSITY

Life history traits of two important lepidopteran pests, the carnation tortrix (*Cacoecimorpha pronubana*) and the light brown apple moth (*Epiphyas postvittana*)

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Declaration

I declare that this thesis is my original work and it has been written by myself. I have acknowledged all the sources of information which have been used in this thesis.

Marcin Wojciech Zielonka

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Abstract

Cacoecimorpha pronubana (Hübner, [1799]) and *Epiphyas postvittana* (Walker, 1863) are economically important polyphagous pest species. Larvae of these moths affect a wide range of horticultural crops. The larva produces silk which it uses to roll leaves creating a shelter against predators and natural enemies, and feeds of the foliage.

The main hypothesis of this study was that different host plant species affect life history traits of *C. pronubana* and *E. postvittana* differently, and that there are differences in life history traits between these two polyphagous species. In order to test the main hypothesis, there were objectives formulated analysing overall abundance and phenology of *C. pronubana* and *E. postvittana*, their oviposition preference, relative performance, and effect of host plants on life history of these two herbivorous species. The main aim of this study was that improved understanding of the life history traits of these two herbivore pest species will help in developing improved integrated pest management systems within horticultural crop habitats.

For this, the effect of abiotic factors on population dynamics and abundance of these species of moth in the ornamental crop habitats was analysed. Further studies involved investigating the life history traits of these two Lepidopterans under controlled environmental conditions at 20°C, relative humidity of 60% and a 16L:8D photoperiod. These included analyses on oviposition preference towards six different ornamental host plant species, the effect of six different host plant species on the larval development and the relationships between different life stages of the insect, as well as the effect of intergenerational dietary changes on the life history traits of both species of moth originating from two different diets.

Noticeable differences were observed between these two species in terms of population dynamics and seasonal appearance based on a five-year study period (2015-2019). Further study showed that oviposition preference in terms of clutch size differed neither between the moth species, nor between the host plants. Larval host plants, however, affected the survival, duration of larval stage, pupal weight and fecundity. It was shown that the longer the duration of larval stage is, the greater the negative effect on female development. Change in larval diet affected oviposition behaviour of both species. Interesting results, however, were identified in the oviposition behaviour in terms of the change in the clutch size, which was affected by transgenerational change in a diet.

It was concluded that better understanding of the population dynamics and the behaviour of these two tortricid (Lepidoptera: Tortricidae) species may be useful in developing forecasting models and in determining crop specific dynamics of these two generalists in developing improved IPM strategies within horticultural crop habitats.

Statement of publications

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Abbreviations

A^o	Open screening area
a.s.l.	Above sea level
°C	Degree of Celsius
cm	Centimetre
CTM	Carnation tortrix moth
df	Degrees of freedom
h	Hour
ha	Hectare
EPPO	European and Mediterranean Plant Protection Organization
IPM	Integrated pest management
LBAM	Light brown apple moth
m	Metres
mm	Millimetres
N	North
na	Not available
%	Percentage
RAF	Royal Air Force
sd	Standard deviation
SEM	Standard error of the mean
UK	United Kingdom of Great Britain and Northern Ireland
USA	United States of America
W	West

Chapter 1. General introduction

Introduction – overview of the thesis

Cacoecimorpha pronubana (Hübner, [1799]) and *Epiphyas postvittana* (Walker, 1863) are economically important pest species. Larvae of these moths affect a wide range of horticultural crops. Damage to the plant is caused by a larva that produces silk which it uses to roll leaves creating a shelter against predators and natural enemies, and feeds of the foliage. Both moths can be seen in Britain flying from April to July, and from August to October, producing two generations per year (Fisher, 1924; Suckling and Brockerhoff, 2010). These pests are highly polyphagous. Together, they affect over 500 plant species that belong mainly to the families Asteraceae, Fabaceae, Oleaceae, Rosaceae, Rutaceae, Solanaceae (Beitia *et al.,* 2016; CABI, 2020) and Griseliniaceae (personal observation).

Despite a wide range of control methods available, there is still a trend to use those pesticides that are often harmful to non-target organisms, or natural environment. In ornamental production pesticide selectivity can be made difficult due to diverse crop habitats in which they are used (Gullino and Wardlow, 1999). Ornamental production nursery is a dynamic agroecosystem comprising of a broad range of different plant species often concentrated within a limited space and time scales. As ecosystems, they are often composed of a number of different habitats each characterised by its own specific microclimate. The use of pesticides may affect the intricate balance between beneficial and non-beneficial organisms living within a crop environment (Gullino and Wardlow 1999; Sterk *et al*., 1999; Biondi *et al.,* 2012). Improved control methods aim to combine the ability to increase natural enemy populations through crop management and conservation approaches in parallel with the introduction of suitable biological control agents (Van Lenteren, 2002). Integrated pest management (IPM) is a control method that has been increasingly important in the management of crop pests. IPM systems provide an alternative to reliance on synthetic pesticides, and are increasingly practiced in ornamental cropping system (Van Lenteren, 2002). IPM programmes typically involve coordinated use of multiple tactics for optimizing the control of a pest in an ecologically and economically sustainable manner (Prokopy, 2003). Importantly, IPM programmes should include a regular monitoring of a pest and natural enemies' populations in crop habitat synchronously considering integration of multiple tactics prior the application of pesticides (Ehler, 2006).

To date, there have been many studies published on Tortricid species that are recognised to be among the most economically important species worldwide (Van der Geest and Evenhuis, 1991, Brown, 2005; Suckling and Brockerhoff, 2010), however, limited information is available on the life history traits of two of the most important Tortricid species in the UK that affect a wide range of ornamental crops – *C. pronubana* and *E. postvittana*. The mechanisms by which ornamental crops affect the life history traits of these two pest species is unclear. The limited information that is available for these pests is general, or it does not apply to the agroecosystem present in the UK. This also means that the information available to growers does not apply to the specific crops, nor does it consider other biotic or abiotic factors that may affect these two pests within a particular crop habitat. This lack of information, as a result, makes difficult to control these insects effectively due to a lack of understanding on which to adapt IPM practices, or improving existing control strategies within IPM programmes appropriate for specific ornamental crops that may be grown together within a plant nursery.

In this thesis, it was hypothesised that biotic and abiotic factors influence life history traits of these two lepidopteran pest species in the ornamental crops located in the UK. As this has not been previously tested, it is hoped that the knowledge gained from this study will help to improve understanding on life history traits of these pests, and contribute to improve existing control strategies for these two Lepidopteran species.

The study presented here investigated the effect of biotic and abiotic factors on life history traits of these two pest species in the ornamental crop habitats. This thesis is a compilation style thesis comprising of seven chapters:

1) The first chapter introduces with an overview of the research programme, the significance of each publication, and a literature review of studied insect species with respect to the species' biology, ecology and control.

2) The second chapter is an experimental chapter that measures abundance and phenology of adult males in the commercial ornamental plant nursery throughout a five-year period between years 2015 and 2019, and compares phenological patterns between these two species of moth, and examine their population dynamics in relation to rainfall, sunshine duration and temperature within ornamental crop habitats.

3) The third chapter is an experimental chapter that measures oviposition preference and fecundity performance of these two species of moth on six different economically important ornamental host plant species under environmentally controlled laboratory conditions.

4) The fourth chapter is an experimental chapter that tests and analyses the effect of six different economically important (often affected) host plant species on the life history parameters of *C. pronubana* under environmentally controlled laboratory conditions, namely on the larval development, subsequently analysing the relationships between different life stages of the insect.

5) The fifth chapter is an experimental chapter that tests and analyses the effect of six different economically important (often affected by this pest) host plant species on the life history parameters of *E. postvittana* in the laboratory conditions, namely on the larval development, subsequently analysing the relationships between different life stages of the insect.

6) The sixth chapter is an experimental chapter that investigates whether the parental host plant environment during larval development can affect growth and reproduction of offspring transgenerationally. The experiment uses three economically important, often affected by these pests, host plant species – *Prunus*, *Griselinia* and *Choisya*.

7) The seventh chapter provides a general discussion that summarises the work presented in this thesis, providing conclusions and recommendations for further studies in this area.

A review of the biology, ecology and control of *C. pronubana* and *E. postvittana* (Lepidoptera: Tortricidae)

1.1. The Tortricidae

The Tortricidae (Latreille, 1803) family of Lepidoptera (Linnaeus, 1758) contains over 1070 genera and more than 10380 species (Van Nieukerken *et al.,* 2011) of which just over 9000 are described. The Tortricidae are the single most important family of moths with many species considered as pests of agricultural, forest and horticultural plants. The family consists of three subfamilies: Chlidanotinae, Tortricinae and Olethreutinae (Brown, 2005).

The codling moth, *Cydia pomonella* (Linnaeus, 1758), the spruce budworm *Choristoneura* sp. Lederer, 1859, and the oriental fruit moth or peach moth, *Grapholita molesta* (Busck, 1916) are considered to be among the most economically important species worldwide (Van der Geest and Evenhuis, 1991), whereas in the UK the most economically important species are the carnation tortrix moth, *Cacoecimorpha pronubana* (Hübner, [1799]) and the light brown apple moth, *Epiphyas postvittana* (Walker, 1863) (CABI, 2020).

Life history stages of this family include an egg, larval (caterpillar), pupal and an imago (adult) stage. Eggs are deposited on the plant parts or other surfaces, singly or in clutches, as the larvae develops inside the egg, the colour of the egg changes. On hatching, the larvae search for a suitable site to feed on the foliage or a fruit of the host plant on which it develops. Initially, the colour of the larvae is often pale yellow or pale green, and the body is divided into segments. The larva passes through several instars during which it sheds its skin. Metamorphosis occurs during the pupal stage after which adults emerge (Fisher, 1924; Geier, 1963; Brown, 2005). The only single apomorphy that unites the family Tortricidae is the structure of the female ovipositor, which is not telescopic, with broad, flat, hairy ovipositor lobes and relatively short apophyses (Horak, 1998).

1.2. Carnation Tortrix Moth (*Cacoecimorpha pronubana*)

Synonyms: *Tortrix* (= *Cacoecia*) *pronubana*, Hb. *Tortrix ambustana* Frölich, 1830; *Tortrix hermineana* Duponchel, 1835; *Tortrix insolatana* H. Lucas, 1848; *Tortrix perochreana* Herrich-Schäffer, 1856 (Fisher, 1924; Imre, 2019)

The carnation tortrix moth *Cacoecimorpha pronubana* (Hübner, [1799]) is recognised as one of the most important pests in ornamental crops (Heungens and Van Daele, 1981; Woodford *et al.,* 1997; Mertens, 1998; Quaglia, 1993; Pencheva and Yovkova, 2016). It is an adventive species, first recorded in Britain on the south coast at Eastbourne in 1905, however, as the species is of continental origin (Europe), it was recorded for the first time in 1797 by Jacob Hübner. The first recorded host plant species of *C. pronubana* in Britain was *Euonymus* (Fisher, 1924), since when it has spread over a large part of the British Isles, feeding on a number of different host pants (UKM, 2020). As the general life history of the species was described by Adkin between 1906 and 1908, Fisher (1924) investigated it further with special reference to the larval and pupal stages of *C. pronubana*.

The carnation tortrix moth naturally occurs in the Mediterranean area. It is a multivoltine species producing at least five generations per year in warmer regions (e.g., Morocco), or four generations per year in Spain or Italy. In the UK, the species produces two generations per year (Fisher, 1924). In spring adults can be observed flying from April when they mate and lay eggs. The first generation can be observed between May and June (summer generation), and the second in around August (winter generation) (Fisher, 1924; Gratwick, 1992). At average temperatures of 15 and 30°C, the complete life cycle takes 123–147 and 28–44 days, respectively (EPPO, 2020). Adults of this moth species vary in size – the male measures typically from 15–17 mm in a wingspan, and female from 18–22 mm. In the male, forewings are warm brown in colour, faintly reticulated with darker brown, with a broad rich red-brown fascia from the middle of the costa, where it is narrowest to the inner margin where it broadens out. Hind wings are bright orange with black borders and a few black scales scattered along the veins. Cilia of the forewings are brown-orange, and of the hind wings are pale orange in colour. The female is more sombre in colour and slightly paler than the male, and reticulations are more clearly defined. The brown fascia is of a duller and less red-brown colour, and its central part is typically indicated only in outline as is also the triangular patch of the apical and hind marginal part. The cilia of the front wings are brown from the apex shading into orange colour towards the anal angle. Those of the hind wings are orange in colour (Fisher, 1924). Longevity of adults is about 11–12 days for females and 14–18 days for males. The lower temperature threshold for copulation is 10.5°C (CABI, 2020). The moth remains inactive during the day, but it can often be observed flying in numbers in the early morning sun or summer evenings (Fisher, 1924). The adults can disperse locally within known habitats or colonise new ones further afield. *Cacoecimorpha pronubana* can affect over 138 plant genera (Kacar and Ulusoy, 2008; Pencheva and Yovkova, 2016; Reddy, 2016) of which many are horticultural or ornamental crops belonging to the families Aceraceae, Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Ericaceae, Fabaceae, Geraniaceae, Oleaceae, Rutaceae, Rosaceae, Salicaceae and Solanaceae (EPPO, 2020; Beitia *et al.,* 2016). In international trade *C. pronubana* may be carried on plants such as carnations, *Dianthus* spp. (Caryophyllales: Caryophyllaceae), chrysanthemums, *Chrysanthemum* spp. (Asterales: Asteraceae), pelargoniums, *Pelargonium* spp. (Geraniales: Geraniaceae), roses, *Rosa* spp. (Rosales: Rosaceae) and other host plants (CABI, 2020).

The female deposits her eggs shortly after mating. Egg laying lasts approximately from 12–14 days for a single female (Fisher, 1924) with a lower temperature threshold for oviposition of 12–13°C (CABI, 2020). Eggs are laid in clutches of various sizes (rarely singly). First clutches are the largest and can contain as many as 200 eggs (Fisher, 1924). On average (mean), females lay clutches of 92 eggs in a glasshouse or 212 in laboratory conditions (Burges and Jarrett, 1976; Pandolfo and Zagami, 1983). Egg clutches are usually oval or round, flattened and scale-like but can vary depending on the surface or shape of a leaf on which they are deposited (Fisher, 1924). The eggs are initially light green, becoming yellow as they develop. Incubation period depends on various factors, but it can range typically between 12 and 24 days (Fisher, 1924; Cameron, 1939). Each female can lay up to 700 eggs (CABI, 2020).

The lower temperature threshold for hatching is about 14°C (CABI, 2020). There are seven larval instars (Fisher, 1924) and larval development lasts between 19 and 91 days, depending on the temperature (Cameron, 1939; Pandolfo and Zagami, 1983). The larvae of this polyphagous herbivore are positively phototrophic (Fisher, 1924). In cooler climates it feeds mainly on the foliage of greenhouse plants (Cameron, 1939). The larva produces silk which it uses to roll leaves together in order to create a shelter where it can feed on the upper epidermis of the leaf (Fisher, 1924). When the leaves are not suitable for rolling, neonate larvae can feed on the undersides of the leaves or move into flowers (Burges and

Jarrett, 1976). In the UK, the species overwinters as first or mainly second-generation larvae (Fisher, 1924); however, mortality may be as high as 70–90% in the winter due to low temperatures and rain (CABI, 2020).

Pupation takes place in a densely created cocoon in a tightly rolled leaf. At first, the pupa is light brown in colour which darkens throughout its development. The size varies from 9–12 mm, although the female pupa is larger than that of the male. The pupal period can vary significantly and can lasts between 4 and 45 days, depending on the temperature (Fisher, 1924; CABI, 2020). The pupae have no importance in overwintering as it would not survive below the temperature of 0°C. In the summer the pupal stage can last for about 10–45 days, whereas in the second generation for about 4–30 days (CABI, 2020), but mostly it is about 14 days (Cameron, 1939), and about 15–17 days (Fisher, 1924), respectively.

1.3. Light Brown Apple Moth (*Epiphyas postvittana*)

Synonyms: *Archips postvittanus* (Walker, 1863), *Austrotortrix postvittana* (Walker, 1863), *Cacoecia postvittana* (Walker, 1863), *Teras postvittana* (Walker, 1863), *Tortrix postvittana* (Walker, 1863)

The light brown apple moth, *Epiphyas postvittana* (Lepidoptera: Tortricidae) (Walker, 1863), similarly to *C. pronubana*, is an important polyphagous herbivore pest species, although, it naturally occurs in Australia where it predominantly affects apple orchards (Danthanarayana, 1975; Suckling and Brockerhoff, 2010). The species has been distributed via trade routes with plant material throughout much of the world, from Tasmania and New Zealand to the USA (Dumbleton, 1940; Rizvi and Raman, 2017; Lo *et al.,* 2018; Retallack *et al.,* 2018.). In the UK, it was first reported in the 1930's in Cornwall and since then it has spread northwards where it also reproduces in nature (CABI, 2020; EPPO, 2020).

In Australia (Victoria) and New Zealand there are three generations per year (Danthanarayana, 1975), whereas in the UK there are typically two generations per year with adult flying from April to July (summer generation) and from August to October (winter generation) (Fountain and Cross, 2007). *Epiphyas postvittana* are highly sexually dimorphic (CABI, 2020; YM, 2020). The adult male is usually smaller than the female with a wing expanse on average of 19 mm (11.6–24.3 mm), and 20 mm (11.8–27.2 mm), respectively. Female fecundity varies greatly and can range from none to over 1490 eggs laid per female, and this variation depends on many different factors, such as host plant quality, temperature or humidity. Most eggs are laid by the two- to three-day-old adult female in one day, accounting for up to 50% total fecundity, and it will reach 80% by the time the female is seven days old (Danthanarayana, 1975). The moth affects a wide range of woody and herbaceous plants from over 363 plant genera. Many are horticultural crops (Suckling and Brockerhoff, 2010; Brockerhoff *et al.,* 2011) belonging to the families Asteraceae, Cannabaceae, Celastraceae, Fabaceae, (CABI, 2020), Griseliniaceae (personal observation), Grossulariaceae, Lamiaceae, Lauraceae, Oleaceae, Pinaceae, Pittosporaceae, Rosaceae, Rutaceae, Sapindaceae, Solanaceae and Vitaceae (CABI, 2020).

Eggs are deposited on the upper surface of leaves in clutches containing typically 3–150 eggs, with 34 eggs per clutch on average as a mean. Eggs are light green, oval and measure approximately 0.84 by 0.95 mm. The lowest temperature threshold for egg development is 7.5°C, with an optimum threshold (95–100% eggs hatched) ranging between 11.5°C and 28°C. The shortest duration of the egg stage (5.7 days) occurs at the temperature of 28°C, whereas at 20°C it takes eight days to hatch (Danthanarayana, 1975).

Neonate larvae of *E. postvittana* are highly mobile. They disperse immediately after hatching in search for a suitable feeding sites, which is a typical behaviour among Tortricidae species. Larvae produce silken thread that is used initially for locomotion – hanging in the air and waiting to be blown by the wind (process called ballooning), and for constructing a shelter by rolling a single leaf, a few leaves together, or webbing leaves to a fruit (Lo *et al.,* 2000). It then feeds on the leaves or fruits causing damage to the plants. There are five (male) or six (female) larval instars, but rarely between five and seven (Danthanarayana, 1975; CABI, 2020). There is no winter resting stage, although overwintering larvae tend to develop slowly, with a lower threshold of development of 7.5°C Danthanarayana, 1975) and an upper of 30°C (Dumbleton, 1939; Danthanarayana, 1975). Duration of larval stage at a temperature of 25°C lasts 18.5 days, and 91 days at 11.5°C (Danthanarayana, 1975).

As in all Tortricid species, pupation takes place inside a cocoon which in-turn is inside rolled leaves. At first the pupa is green to light brown in colour but it darkens during its development. Male pupae vary in size between 2.5 and 7.6 mm, and females between 2.9 and 9.8 mm. The female pupa is heavier than the male pupa, weighing on average 28.9 mg, and 24.1 mg, respectively. Pupation periods depends mainly on temperature and can vary between 11.5 days at 20°C and 16.5 days at 25°C. With temperatures increase from 28°C, 30°C, 31°C, 32°C to 33°C, the pupation success of the larvae gradually decreases from 82%, 30%, 4% to none, respectively (Danthanarayana, 1975).

1.4. Control of the Tortricidae

1.4.1. Pesticides – crop management, environmental concerns and human health

Pesticides have been used for many centuries, since about 1550 B.C., when methods for eliminating fleas were described, through the use of arsenic compounds to control insects in China (900 A.D.), and in the Western World (1669), up till the discovery of synthetic pesticides (Costa, 1987). There have been various products and techniques developed to control the larvae and eggs of *C. pronubana* and *E. postvittana* (Fisher, 1924; Cameron, 1939; Morris, 1950; Suckling *et al.,* 1990; Walker *et al.,* 2017). When in the first half of the twentieth century sprays based on nicotine or lead arsenate, or fumigation with nicotine or hydrocyanic acid gas (Fisher, 1924; Cameron, 1939) gradually become ineffective against the pests, the introduction of tetrachloroethane and carbon bisulphite gave satisfactory control. Later, the pests were controlled by treatments of a wide range of insecticides, including organophosphate, carbamate and synthetic pyrethroid compounds (Cross *et al.,* 2001).

Despite a wide range of available pesticides, pest control can be ineffective (Gullino and Wardlow, 1999). It was observed that, through natural selection and rapid reproduction (Croft and Baan, 1988; Boivin *et al.,* 2003; Lee *et al.,* 2015), pest populations tend to build a resistance to synthetic pesticides, particularly after the prolonged use of the same product (Georghiou and Mellon, 1983; Sarwar and Salman, 2015). For example, the larvae of the codling moth, *C. pomonella* (Linnaeus, 1758) (Lepidoptera: Tortricidae), have developed resistance over the years to organophosphate (azinphos-methyl), pyrethroid, and diacyl hydrazine (DAH) insecticides (Mota-Sanchez *et al.,* 2008). It was later observed that the same larvae developed a cross-resistance with organophosphate insecticides to a neonicotinoid insecticide – acetamiprid (Knight, 2010). *Epiphyas postvittana*, however, was found to be resistant to one of the organophosphate insecticides – azinphos-methyl (Suckling *et al.,* 1984), and it was later shown that the resistance can vary between the strains of the moth (Armstrong and Suckling, 1990). Thus far, no resistance to insecticides has been found for *C. pronubana*.

It was, however, the insidious and continuous negative impact on the environment by pesticides that caused the progressive reduction or elimination of the use of synthetic insecticides (Carson *et al.,* 1962; Suckling *et al.,* 1984; Ahmad and Khan, 2017; Carvalho, 2017). For example, chlorodiphenyltrichloroethane (DDT) (chlorinated hydrocarbon insecticide) was found to be toxic to the environment and human health (Rattner, 2009). Due to long residual efficacy and accumulation through food chain, DDT lead to negative effects in the wildlife (e.g., chronic effects on the nervous system in mammals, or serious birth injury or defects in oviparous animals), and human health in terms of carcinogenicity, acute and persistent injury to the nervous system and reproductive organs, lung damage, dysfunction of the immune and endocrine systems, or birth defect (Thuy, 2015). Similar effects were observed for other products, such as organophosphate, carbamate or pyrethroid pesticides (Markowitz, 1992; Dementi, 1994; Bhatt *et al.,* 1999; Bradberry *et al.,* 2005; Rehman *et al.,* 2014; Silberman and Taylor, 2020). However, novel pesticides gradually become more efficient in targeting particular pest species showing lower toxicity to human health (Grafton-Cardwell, 2005). Still, despite the negative effect of pesticides on human health and the environment, the annual consumption of pesticides worldwide grows significantly every year (Mahmood *et al.,* 2016; Sharma *et al.,* 2019).

As the use of integrated pest management (IPM) systems becomes an alternative to synthetic pesticides, it is not only limited to vegetable crops, but it is increasingly practiced in ornamental crops too (Van Lenteren, 2002). Undesirable side effects of chemical control, such as phytotoxicity and pesticides residual persistence, development of resistance in pests and pathogens, as well as toxicity to predators, natural enemies of pests and to human health, apply to all agroecosystems and should not be neglected (Brown, 1961; Sachs *et al.,* 1987; Gullino and Wardlow 1999; Biondi *et al.,* 2012).

In ornamental production pesticide selectivity can be greatly limited in use within diverse crop habitats (Gullino and Wardlow, 1999). Generally, phytotoxic activity can often be observed on crop plants via pesticides combined in soil (Nash, 1966), or on crop plants where pesticides are applied above the soil or water surface, for example, pearl millet, *Pennisetum americanum* Rich., carrot, *Daucus carota* L., large-leaved lupine, *Lupinus polyphyllus* Lindl. (Harms, 1992), common onions, *Allium cepa* L., (Ogeleka *et al.,* 2016), *Vitis vinifera* L. (Papaioannou-Souliotis *et al.,* 1998), broad range of ornamental plant species (Miller and Uetz, 1998; Bažok and Cenko, 2016; Meena *et al.,* 2016), or common duckweed, *Lemna minor L.* (Peterson *et al.,* 1994). Toxicity can also be observed through the use of pesticides that may be often considered as safe, usually when such pesticides are used too often, or in combination with other products (Gullino and Wardlow, 1999). Toxicity of synthetic pesticides was also observed on arthropod natural enemies (Theiling and Croft, 1988; Roubos *et al.,* 2014). Aydogdu *et al*. (2017), for example, showed that three pyrethroid insecticides based on different active ingredients that are used to control the rose tortrix, *Archips rosana* (Linnaeus, 1758) (Lepidoptera: Tortricidae) are also toxic to the pest’s natural enemies. The use of bio-pesticides, e.g., microbial organisms (bacterial, fungal), secondary metabolites from micro-organisms (antibiotics), plant derived pesticides, or insect pheromones applied for mating disruption, has however, become a promising solution to the problem; they are characterized by a non- or very low toxicity to non-target species, and the likelihood for the pest resistance occurrence to bio-pesticides is non-existent or very low (Copping *et al.,* 2000; Villaverde *et al.,* 2014; Saraf *et al.,* 2013).

1.4.2. Biocontrol and Natural Enemies

The use of pesticides may affect the delicate balance between beneficial and non-beneficial microflora and microfauna within a crop environment (Gullino and Wardlow 1999; Sterk *et al*., 1999; Biondi *et al.,* 2012). Biological control methods, however, aim to combine aspects of attracting natural enemies along with the use of suitable biological control agents (Van Lenteren, 2002) and the use of practices that promote higher plant diversity that enhances the activity of beneficial organisms (Sanguankeo and Leon, 2011).

Bacillus thuringiensis is a widely used, moderately effective biocontrol agent for the larvae of tortricid species, being not harmful to most natural enemies of these pests. Neonates of these herbivores are most susceptible, whereas, mature larvae are more difficult to control (Burges and Jarrett, 1976; Cross *et al.,* 2001). Eggs and larvae are often attacked by parasitic wasps and other predators (Price *at al*., 1980; Hassan, 1993; Cross *et al.,* 2001; Thomson and Hoffmann, 2010; Suckling and Brockerhoff, 2010; Gratwick, 2012; Murray, 2014; Rusch *at al*., 2015; Göttig and Herz, 2016) that play an important role in crop habitats in regulating pest numbers below economical damaging levels. Larvae are also a valuable food source to birds (Brackenbury, 1999). The eggs and larvae of *C. pronubana* and *E. postvittana* are parasitized by a number of different natural enemies. *Cacoecimorpha pronubana* larvae, for example, are often attacked by braconid wasps belonging to the genus *Apanteles* Förster, 1862 and *Macrocentrus* Curtis, 1833 (Hymenoptera: Braconidae), but also by other species belonging to the genus *Itoplectis* (Hymenoptera: Ichneumonidae), *Actia* Robineau-Desvoidy, 1830 and *Nemorilla* Róndani, 1856 (Diptera: Tachinidae), whilst the eggs are commonly parasitized by *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) (Fisher, 1924; Cross *et al.,* 2001; Mifsud *et al.,* 2019). Natural enemies of *E. postvittana* are often found to be species belonging to the genus *Gonius* Forster, 1856 (Hymenoptera: Bethylidae), *Dolichogenidea* Viereck, 1911, *Enytus*, *Campoplex* Gravenhorst, 1829, *Diadegma* Förster, 1869, *Triclistus* Förster, 1869, *Meteorus* Haliday, 1835 (Hymenoptera: Braconidae), and *Pteromalus* Swederus, 1795 (Hymenoptera: Pteromalidae), and the hyperparasite *Gelis* Thunberg, 1827 (Hymenoptera: Ichneumonidae), (Dumbleton, 1940; Danthanarayana, 1980; Shaw, 1981; Yazdani *et al.,* 2015).

Pheromone traps are not only used to monitor moth species within a crop habitat, but are employed as mating disruptors, or for mass trapping, reducing adult males from the particular population of the moth species. A trap contains a lure containing particular sex pheromones that attract a particular species. Insect pests are caught on a sticky base or in a funnel trap (McNeil, 1991; Carde and Minks, 1995; Reddy and Guerrero, 2001; Mochizuki *et al.,* 2002; Cardé and Haynes, 2004; Subchev *et al.,* 2004; Cuthbertson and Murchie, 2005). Even though there are specific synthetic pheromones to control *E.*

postvittana (Csiro, 1982; Bellas *et al.,* 1983), and *C. pronubana* populations (Witzgall and Frérot, 1989; Ostrauskas *et al.,* 2008), a few non-target species may also be caught (Ostrauskas *et al.,* 2008). Interestingly, female-released sex pheromones may also attract larvae of the same species (Zielonka *et al*., 2016).

1.5. Integrated Pest Management – History and definition

First records of pest management occurred in 4700 B.C. with the discovery of silk production from *Bombyx mori* (Linnaeus, 1758) (Lepidoptera: Bombycidae) in China (Orlob, 1973; Peshin and Dhawan, 2009; Abrol and Shankar, 2012), although, according to Chinese records, the silkworm culture first appeared much later, in 2700 B.C. (Cherry, 1993). In 2500 B.C., the use of insecticides was recorded by the Sumerians who used sulphur compounds to control insects. Between the years 324 B.C. and 300 A.D., the Chinese introduced the predatory ants, *Acephali amaragina* and *Oecophylla smaragdina* Fabricius, 1775 (Hymenoptera: Formicidae) in citrus trees to manage caterpillars and large boring insects, whereas around 200 B.C. Romans promoted oil sprays for pest control. A wealth of information on pest management was produced between years 1100 and 1200 A.D., and was subsequently described by Ibn Al-Awam in his classic book on agriculture. In 1763, Carl Linnaeus published a prize-winning essay that suggested using mechanical and biological control to manage orchard caterpillars.

Since the agricultural revolution took place in Europe in 1750–1880, crop protection has become more extensive and intensive. This was initiated through the discovery and introduction of new machinery, and followed by the discovery and introduction of new biological and synthetic pesticides (Orlob, 1973; Peshin and Dhawan, 2009; Abrol and Shankar, 2012) and genetically modified organisms (GMOs) (Woolsey, 2012). Over the last 60 years, integrated pest management has become a widely recognised plant protection strategy. Following the discovery and introduction of synthetic pesticides in the 1940s, it took nearly two decades for scientists to note a negative impact of pesticides on natural environment. As it was later observed, due to deleterious effects of insecticides on pest's natural enemies, and the development of resistance of pests to pesticides, a new concept of IPM was introduced in the 1950s (Peshin and Dhawan, 2009).

Numerous definitions of IPM have been proposed over the years. In the early days integrated control was defined by Stern *et al*. in 1959 as an "application of pest control which combines and integrates biological and chemical control. Chemical control is used as necessary, and in a manner, which is least disruptive to biological control. Integrated control may make use of naturally occurring biological control as well as biological control effected by manipulated or induced biotic agents" (Coll and Wajnberg, 2017, p.4). After the introduction in 1959 of the concepts of economic thresholds (ET), economic injury levels (EIL), and integrated control (IC) (Orlob, 1973; Peshin and Dhawan, 2009; Abrol and Shankar, 2012), the concept of IC, originally limited to the combination of chemical and biological control methods, was precisely defined in 1965 at a symposium sponsored by the Food and Agriculture Organization (FAO), of the United Nations, held in Rome, Italy. Later, in 1966 'integrated pest control' was formulated by Smith and Reynolds as a "pest population management system that utilizes all suitable techniques in a compatible manner to reduce pest populations and maintain them below economic injury level" (EIL) (Coll and Wajnberg, 2017, p.4). The full expression of the concept behind IPM was first published in 1972 (Bajwa and Kogan, 2002). Bottrell and Bottrell (1979), however, determined IPM as the selection, integration and implementation of pest control based on predicted economic, ecological and sociological consequences. As that author indicated, IPM should make maximum use of naturally occurring control agents, including weather, crop habitat diversity, predators and natural enemies of a pest or disease (Bottrell and Bottrell, 1979). In the socioeconomic context of farming systems, Bottrell and Bottrell (1979) and Dent (1995) referred to the earlier definitions of IPM, and stated that all suitable techniques are required in order to maintain the pest population levels below EIL (Bottrell and Bottrell, 1979; Dent, 1995). Bajwa and Kogan (2002) later referred to a crop protection or pest management system with implication for methodological and disciplinary integration as a sustainable approach with a sound ecological foundation, which is generally targeted against the entire complex of an agroecosystem (Bajwa and Kogan, 2002). Over a decade ago, however, integrated pest management was proposed by Prokopy (2003) as a "decision-based process involving coordinated use of multiple tactics for optimizing the control of all classes of pests (insects, pathogens, weeds, vertebrates) in an ecologically and economically sound manner" (Prokopy, 2003, p.299). As Ehler (2006) further explained, regular monitoring of pest and natural enemies' populations in crop habitat is an important factor when IPM strategies are practiced. However, economic or injury levels thresholds, as well as integration of multiple tactics prior the application of pesticides should be considered synchronously (Ehler, 2006). Lefebvre *et al*. (2015) later summarised, that IPM should be defined as "a system based on three main principles: (i) the use and integration of measures that discourage the development of populations of harmful organisms (prevention); (ii) the careful consideration of all available plant protection methods; and (iii) their use to levels that are economically and ecologically justified" (Lefebvre *et al.,* 2015, p.2).

1.6. Invasive species

Horticulturists face a great diversity of pests daily, those known species and those newly introduced to crops. As pests can be introduced to a crop with a new or non-native plant material (Gullino and Wardlow, 1999), such alien species may create novel tri-trophic interactions with native plants and indigenous natural enemies (Wang *et al.,* 2013), which in consequence may create new challenges within IPM practices. For example, *E. postvittana* population, being an invasive species in California, faces a steady decline, perhaps due to the presence of naturally occurring indigenous enemies (Wang *et al.,* 2019). Climate change may play an important part in the appearance of new invasive species in the UK (Malumphy, 2012), which may require new approaches within IPM strategies (Larson *et al.,* 2011). A number of plant diseases (e.g., plant viruses) can be transmitted by insect species as it has been shown for, for example, the western flower thrip, *Frankliniella occidentalis* Pergande 1895, and the silverleaf whitefly, *Bemisia tabaci* (Gennadius, 1889) (Gullino and Wardlow, 1999).

1.7. Thesis aims and objectives

Aims: The aim of this study was to improve understanding of the life history traits of the carnation tortrix (*Cacoecimorpha pronubana*) and the light brown apple moth (*Epiphyas postvittana*), two polyphagous pest species of moth, and to contribute to improving integrated pest management systems within horticultural crop habitats.

Hypothesis: Biotic and abiotic factors influence life history traits of these two lepidopteran pest species in the ornamental crop habitats.

Objectives: The specific objectives of this study were to:

1. Measure the abundance of adult males throughout a five-year period between 2015 and 2019, and compare and detect phenological patterns between these two species of moth intra- and interseasonaly, and examine their population dynamics in relation to rainfall, sunshine duration and temperature within ornamental crop habitats.

2. Test oviposition preference of these two species of moth towards six different ornamental host plant species under the controlled laboratory conditions through analysing, measuring and determining fecundity performance of the adult females.

3. Test the effect of six different host plant species on the life history parameters of *C. pronubana* and *E. postvittana* under the controlled laboratory conditions, namely on the larval development of each of these two pest species, subsequently analysing the relationships between different life stages of the insect.

4. Test the effect of intergenerational dietary changes under the controlled laboratory conditions on the life history traits of the offspring of these two species of moth originating from two different diet regimes (larval parental diets).

Chapter 2. Abundance and phenology of two moth species, *Cacoecimorpha pronubana* and *Epiphyas postvittana* (Lepidoptera: Tortricidae).

2.1. Abstract

Cacoecimorpha pronubana (Hübner, [1799]) and *Epiphyas postvittana* (Walker, 1863) are economically important polyphagous pest species. The larvae of these moths affect a wide range of horticultural crops. The seasonal abundance and population dynamics of these two species was evaluated, hypothesising that both species of moth exhibit similar patterns in their seasonal abundance and respond to abiotic factors. The study was carried out on a wide range of protected ornamental crops grown on a total area of one hectare at a commercial nursery. The study was completed over five consecutive years from 2015 to 2019, where both populations were monitored weekly during the months of moth activity, from April to November, using sex pheromone traps to trap the males of both species. The timing and abundance of catches were analysed in relation to local meteorological data. The mean yearly abundance of adult males was 604 ± 23.89 (mean ± SE; *C. pronubana*) and 1706 ± 167.18 (*E. postvittana*) also differing significantly between years for both species. There was no influence of any weather measures on the abundance of *E. postvittana*, but sunshine duration (4.84 ± 0.26 hours) and temperature (13.04 ± 0.57 °C) affected the mean seasonal abundance of *C. pronubana.* There was an overall difference in the seasonal pattern of abundance between the species studied. While a seasonal abundance difference between years for *C. pronubana* was demonstrated, no significant seasonal differences for *E. postvittana* was found. Improved understanding of seasonal abundance, phenological patterns and inter-seasonal variations in population dynamics of these two species may be useful in developing forecasting models that can be used in improving integrated pest management strategies for these two pests.

2.2. Introduction

The carnation tortrix moth (CTM), *Cacoecimorpha pronubana* (Lepidoptera: Tortricidae) and the light brown apple moth (LBAM), *Epiphyas postvittana* (Lepidoptera: Tortricidae) are economically important pest species affecting a wide range of horticultural crops (Fisher, 1924; Speyer, 1938; Beitia *et al.,* 2016; New, 2016). Both species of moth are cosmopolitan pests and are naturalised adventive species in the UK (CABI, 2020; Gilligan *et al.,* 2020). Damage to the plant is caused by the larva that feeds on the foliage. It produces silk, which it uses to roll leaves together creating a shelter (Fisher, 1924; Cameron, 1939). *Cacoecimorpha pronubana* can produce at least five generations per year in warmer regions (North Africa), or four generations per year in Spain or Italy. In the UK, the species produces two generations per year overwintering as first or mainly second-generation larvae (Fisher, 1924). *Epiphyas postvittana* produces three to four generations per year in Australia, where the moth is a native species (Danthanarayana; 1983). In the UK, *E. postvittana* typically has two generations per year (Suckling and Brockerhoff, 2010). There is, however, no winter resting stage for LBAM, although overwintering larvae tend to develop slowly with a lower threshold of development for all stages of 7.5°C and an upper threshold of 31°C (Danthanarayana; 1975). Both moths can be seen in Britain flying from April to July, and from August to October (Fisher, 1924; Suckling and Brockerhoff, 2010).

The population dynamics and the seasonal abundance of these two insect pest species is dependent on numerous biotic and abiotic factors. Eggs and larvae of Tortricidae species are naturally controlled by parasitic wasps and other insects (Price *at al*., 1980; Hassan, 1993; Thomson and Hoffmann, 2010; Murray, 2014; Rusch *at al*., 2015; Göttig and Herz, 2016). Eggs and larvae of *C. pronubana*, for example, can be parasitized by *Trichogramma sp*. and *Apanteles sp*., respectively (Solomon *et al.,* 2001). Such phenomena, however, are also governed by environmental conditions (e.g., precipitations, sunshine duration, temperature or humidity) upon which performance of both prey and predators depends (Thiéry *et al.,* 2018). For example, at average temperatures of 15°C and 30°C, the complete life cycle of *C. pronubana* ranges between 123–147 and 28–44 days, respectively. In addition to slower development, low temperatures and rain may increase larval mortality up to 70–90% (CABI, 2020). Changes in air temperature can also affect the flight duration of the adult moth. It was shown that the longest flight duration for both sexes of *E. postvittana* occurs at 20°C and relative humidity of 60%, but an increase of atmospheric humidity can significantly decrease the flight duration of females (Danthanarayana and Gu, 1992). Abiotic factors can also affect the development of natural enemies of Lepidopterans. For example, the pupal survival, parasitism rates, longevity and fecundity of the parasitoid, *Apanteles hemara* (Nixon) (Hymenoptera: Braconidae) significantly decrease with increasing temperature (Agbodzavu *et al.,* 2020).

The choice of control methods of these species of moth depends on their life stage, and whether an integrated pest management (IPM) approach has been adopted. The egg and larval stages of these two pests are controlled mainly by the use of synthetic pesticides (e.g., neonicotinoids and pyrethroids), bio-pesticides (e.g., *Bacillus thuringiensis* Berliner, 1915), or natural enemies (Suckling and Brockerhoff, 2010; Wearing *et al.,* 2012; Reddy, 2016). Monitoring is recognised as an essential component of any IPM programme. It helps to evaluate pest population dynamics, their potential outbreaks, improving the timing of the application of control measures and may allow for the selection of the most sustainable control strategy (Wearing *et al.,* 2012). The most efficient monitoring method of both populations of these moths are pheromone traps. Traps are baited with a specific female sex pheromone that attracts male adults of the same species. Traps are used not only for monitoring and data collection purposes (Guda and Capizzi, 1988; Suckling *et al.,* 2015), but also for mass-trapping of males to disrupt mating, thereby reducing offspring production in female adults (Quaglia, 1993; Suckling *et al.,* 1994; Suckling *et al.,* 2014).

The objective of this study was to evaluate the seasonal abundance of two species of moth, *C. pronubana* and *E. postvittana* in relation to rainfall, sunshine duration and temperature during a five-year study period. It was hypothesised that both species would exhibit similar phenological population patterns, in terms of seasonal abundance both within and between seasons, and that the pattern of abundance for both species would be significantly affected by the three abovementioned abiotic factors. Results from this study may be useful in developing forecasting models, which in turn would be useful within integrated pest management programmes for these two herbivorous species in the ornamental crop habitats.

2.3. Materials and Methods

2.3.1. Data collection and pheromone traps

This study was carried out at an ornamental plant nursery in Shropshire, UK (52°37’20’’ N, 2°15’20’’ W; 119 m a.s.l.) on a wide range of continuously ventilated protected ornamental crops grown in 2–10 litres black polythene pots. All sides of polytunnels remained open each season for the entire five-year study period. Crop plants included species from the families Araliaceae, Buxaceae, Caprifoliaceae, Celastraceae, Escalloniaceae, Garryaceae, Griseliniaceae, Hypericacaeae, Lamiaceae, Pittosporaceae, Plantaginaceae, Rhamnaceae, Rosaceae and Rutaceae. The height of the crop plants ranged between 20 cm to 80 cm.

Two populations of moth species – *C. pronubana* and *E. postvittana* were monitored weekly from April to November in each of five years (2015 to 2019). Monitoring was carried out using Agralan ® Pheromone Trapping System (Agralan Ltd, Wiltshire, UK), consisting of open-sided delta traps baited with a synthetic female sex pheromone lure. Each trap was baited with one lure containing either *C. pronubana* (Z11-14Ac, E11-14Ac, Z11-14OH, Z9-14Ac) or *E. postvittana* (E11-14Ac, E9E11-14Ac) synthetised female sex pheromone, respectively, to attract males of the same species (Agralan Ltd, Wiltshire, UK).

The numbers of male individuals caught in each trap was recorded weekly. A total of 26 moth traps were deployed, 13 for each species in each year of the study. Traps were placed in polytunnels of a total area of approximately one hectare, within a 16-hectare nursery site. Two traps were used per polytunnel, one trap for each species of moth. Traps were hung on a string just above crop height with a distance of at least 50 metres between each trap adhering to spacing instructions from the Agralan ® Pheromone Trapping System supplier (Agralan Ltd, Wiltshire, UK), and similar to other studies (David *et al.,* 1982; David *et al.,* 1983; Perry and Wall, 1984).

Pheromone lures were replaced four times per year in each trap for each moth species between April and November. Non-target species of moth occasionally caught in traps were also recorded. Pyrethroid insecticides (deltamethrins) and natural pyrethrins were used throughout each of the growing seasons in order to prevent pest populations from exceeding economic injury levels in each of the crops being monitored (Higley and Wintersteen, 1992; Pedigo and Higley, 1992; Peterson *et al.,* 2018). The economic threshold for both species of moth is a catch of over 30 adult male moths caught per pheromone trap per week (AHDB, 2020). Pest management practices initiated by growers are made regardless of the plant growth stage.

The ‘seasonal abundance’ term used in this thesis indicates the number of adult males caught in traps recorded in each week over the given season. The ‘season’ term used here indicates the period of 32 weeks that begins from week 14 and ends in week 45 for each calendar year during the study. The ‘pattern of the seasonal abundance’ phrase used in this paper indicates the seasonal distribution of abundance recorded for adult males caught in traps over the given season, and may be used in order to distinguish certain phenological characteristics in this respect.

2.3.2. Meteorological data

Meteorological data for the years 2015–2019 were obtained from the weather station nearest to the study site (~33 km), located in RAF Shawbury, UK (52°47’38’’ N, 2°39’47’’ W; 72 m a.s.l.). Data were supplied by MetOffice, and consisted of daily total rainfall (0900–0900), daily total sunshine (0100–2400), and daily mean temperature (0900–0900) measured in millimetres, hours, and degrees Celsius, respectively. Sunshine data were taken from a Campbell Stokes recorder located at the abovementioned weather station. Data were converted into weekly means for statistical analyses.

2.3.3. Statistical analyses

Statistical analysis was performed in order to evaluate the seasonal abundance of each moth species, and to compare their abundance within and between seasons. It was also analysed the correlation between the seasonal abundance of each species and abiotic factors: precipitation, sunshine duration, and temperature. None of the data were normally distributed (Shapiro-Wilk test, all $P < 0.05$) and did not meet homogeneity of variance assumptions (Levene's test, $P < 0.05$). Thus, analyses were performed using non-parametric tests. The unpaired two-samples Wilcoxon rank sum test with continuity correction (Mann-Whitney U-test) was used to compare the overall difference in abundance between the two moth species for the entire study. The Kruskal-Wallis test was used to test intra-seasonal differences in moth abundance between weeks within seasons, as well as inter-seasonal differences in the moth abundance between years. The spearman rank correlation test was used to evaluate the association between the moths and three abiotic factors (estimating a rank-based measure of association with Spearman's rho coefficient). All statistical tests were performed using R version 4.0.2 (R Core Team, 2020), and the significance level was set at $\alpha=0.05$.

2.4. Results

Number of male moths recorded

The average yearly abundance of *C. pronubana* adult males caught over the five-year study period (2015–2019) was 604 ± 23.89 (mean ± SE) which was 2.82 times less than the average yearly abundance of *E. Postvittana* (1706 ± 167.18). The difference was statistically significant (Wilcoxon test: $W = 169$, $P < 0.0001$). The average weekly abundance of adult males per year was (mean ± SE) 45 ± 0.57, 159 ± 0.79, 104 ± 0.81, 183 ± 1.54 and 113 ± 0.72 for *C. pronubana*, and 69 ± 0.62, 930 ± 4.16, 500 ± 2.78, 102 ± 0.93 and 105 ± 0.57 for *E. postvittana* for 2015, 2016, 2017, 2018 and 2019, respectively.

Intra-seasonal pattern of abundance

The mean weekly abundance varied significantly overall for both species of moth (Kruskal-Wallis chi-squared [KW]: $\chi^2 = 20.8$, $df = 4$, $P = 0.0003$, *C. pronubana*; KW: $\chi^2 = 68.8$, $df = 4$, $P < 0.0001$, *E. postvittana*). Comparing the yearly abundance of each moth species it was found a significant difference only for the years 2016 and 2017, (Wilcoxon test: $W = 95.5$, $P < 0.0001$; and $W = 229.0$, $P = 0.0001$) (Figure 2.1).

Inter-seasonal differences in moth abundance (weekly five-year cumulative)

The average number of male moths caught each week differed significantly for *C. Pronubana* (KW: $\chi^2 = 71.0$, df = 31, $P < 0.0001$). By contrast, weekly catches throughout the five-year period did not differ significantly overall for *E. postvittana* (KW: $\chi^2 = 34.5$, df = 31, $P = 0.304$) (Figure 2.2). A cumulative seasonal abundance for both moths can be observed in Figure 2A and 2B. Two common characteristic patterns of the seasonal abundance between the species are reflected in two generational peaks; observed throughout the seasons, each of the peaks represents the rise in the mean number of males caught. For both moths, there was a gradual rise in trap catches between weeks 18–22, and then there was a second shorter period where there was a more pronounced increase in trap catches between weeks 29–30 for *C. pronubana*, and between weeks 31–32 for *E. postvittana*.

Correlation between cumulative seasonal moth abundance and abiotic factors

While overall abundance for *C. pronubana* across all years 2015–2019 was not significantly correlated with precipitation (Spearman's rank correlation [SRC]: S = 5568.7, $P = 0.911$, ρ (rho coefficient) = -0.021; Figure 2.3A), it was significantly correlated with mean sunshine duration (SRC: S = 3046, $P < 0.01$, $\rho = 0.44$), and with mean temperature (SRC: S = 1882, $P < 0.0001$, $\rho = 0.66$) (Figure 2.3B and 2.3C). Precipitation, mean sunshine, nor temperature were correlated with *E. postvittana* abundance in this study (all $P > 0.05$; Figure 2.3D–2.3F). With respect to the seasons (means ± SE), sunshine duration (5.46 ± 0.57) affected only *C. pronubana* in 2018 (SRC: S = 2329, $P = 0.0006$, $\rho = 0.57$). Temperature was significantly correlated with abundance in both species for some years, *C. pronubana* in 2015 (12.32 ± 0.49), 2016 (13.01 ± 0.70), 2018 (13.70 ± 0.67) and 2019 (12.82 ± 0.68), (SRC: S = 3512, $P = 0.045$, $\rho = 0.36$; S = 1681, $P < 0.0001$, $\rho = 0.69$; S = 2018, $P = 0.0001$, $\rho = 0.63$; S = 2651, $P = 0.003$, $\rho = 0.51$) respectively, and *E. postvittana* in 2017 (13.34 ± 0.58) (SRC: S = 2641, $P = 0.003$, $\rho = 0.52$) (Table 2.1).

Correlation between two species of moth in cumulative seasonal abundance

There was a significant correlation between the cumulative seasonal abundance of the two moth species (SRC: S = 2034, $P = 0.0001$, $\rho = 0.63$), as well as between the overall abundance of both species combined, and individual *C. pronubana* (SRC: S = 833, $P < 0.0001$, $\rho = 0.52$), and *E. postvittana* (SRC: S = 449, $P < 0.0001$, $\rho = 0.92$) (Figure 2.3G–2.3I).

Table 2.1. Correlation between the mean seasonal abundance of two species of moth, *Cacoecimorpha pronubana* (CTM) and *Epiphyas postvittana* (LBAM), and mean abiotic factors for five consecutive years (means ± SE). Spearman rank correlation test was used to evaluate the association between the moths and three types of abiotic factors.

Abiotic factors for given year (means ± SEM)			CTM		LBAM	
			rho	P - value	rho	P - value
Precipitation [mm]	2015	1.68±0.19	0.02	0.909	-0.08	0.665
	2016	1.83±0.31	0.07	0.695	-0.25	0.161
	2017	1.86±0.29	0.09	0.635	-0.03	0.884
	2018	1.57±0.34	-0.12	0.5314	-0.07	0.708
	2019	2.64±0.51	-0.05	0.0778	-0.06	0.744
Sunshine [hours]	2015	5.13±0.41	0.21	0.242	0.11	0.547
	2016	4.88±0.31	0.19	0.302	0.08	0.672
	2017	4.39±0.38	0.21	0.259	0.32	0.071
	2018	5.46±0.57	0.57	0.0006	0.22	0.233
	2019	4.34±0.37	0.33	0.062	0.34	0.055
Temperature [°C]	2015	12.32±0.49	0.36	0.045	0.26	0.148
	2016	13.01±0.70	0.69	<0.0001	0.28	0.118
	2017	13.34±0.58	0.35	0.053	0.52	0.003
	2018	13.70±0.67	0.63	0.0001	0.03	0.866
	2019	12.82±0.68	0.51	0.003	0.34	0.055

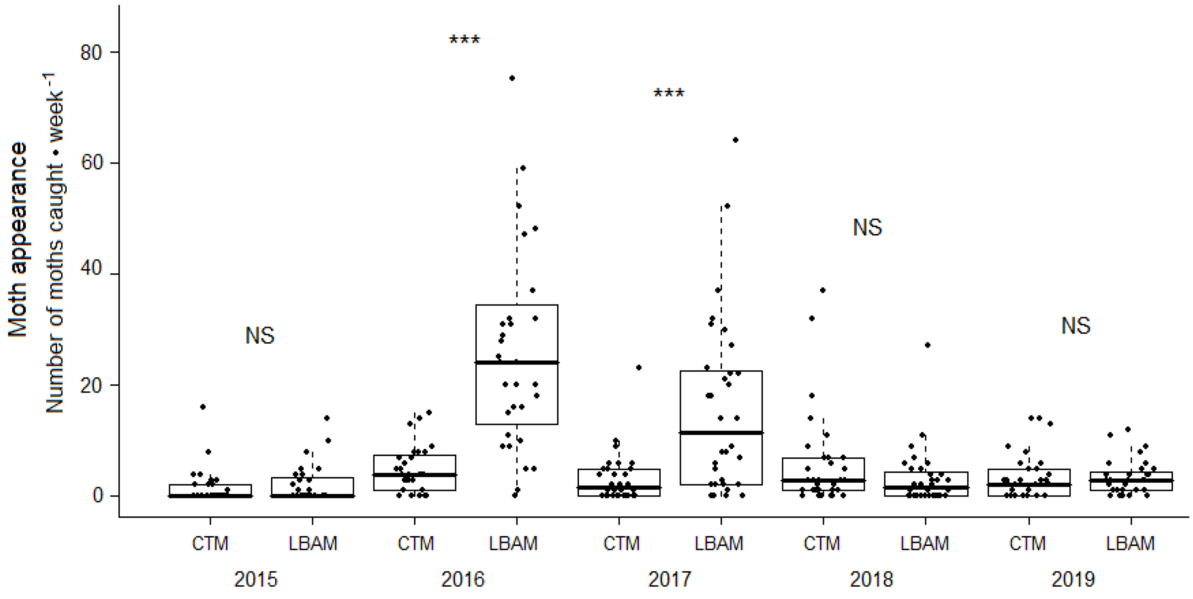


Figure 2.1. Number of male moths recorded for each year between 2015 and 2019, for *Cacoecimorpha pronubana* (CTM) and *Epiphyas postvittana* (LBAM). Statistical analyses were performed using Wilcoxon rank sum test with continuity correction in order to compare the number of moths caught in any given year between the moths; ^{NS} P > 0.05, * P < 0.05, ** P < 0.01, *** P < 0.0001. Boxes represent the interquartile range (IQR) with a thick horizontal line at the median and whiskers extending to the extrema of the observations falling within 1.5 IQRs of the upper or lower quantiles. Black scattered dots represent data points spread horizontally for each box & whisker in order to show the distribution of data for each moth in a given year.

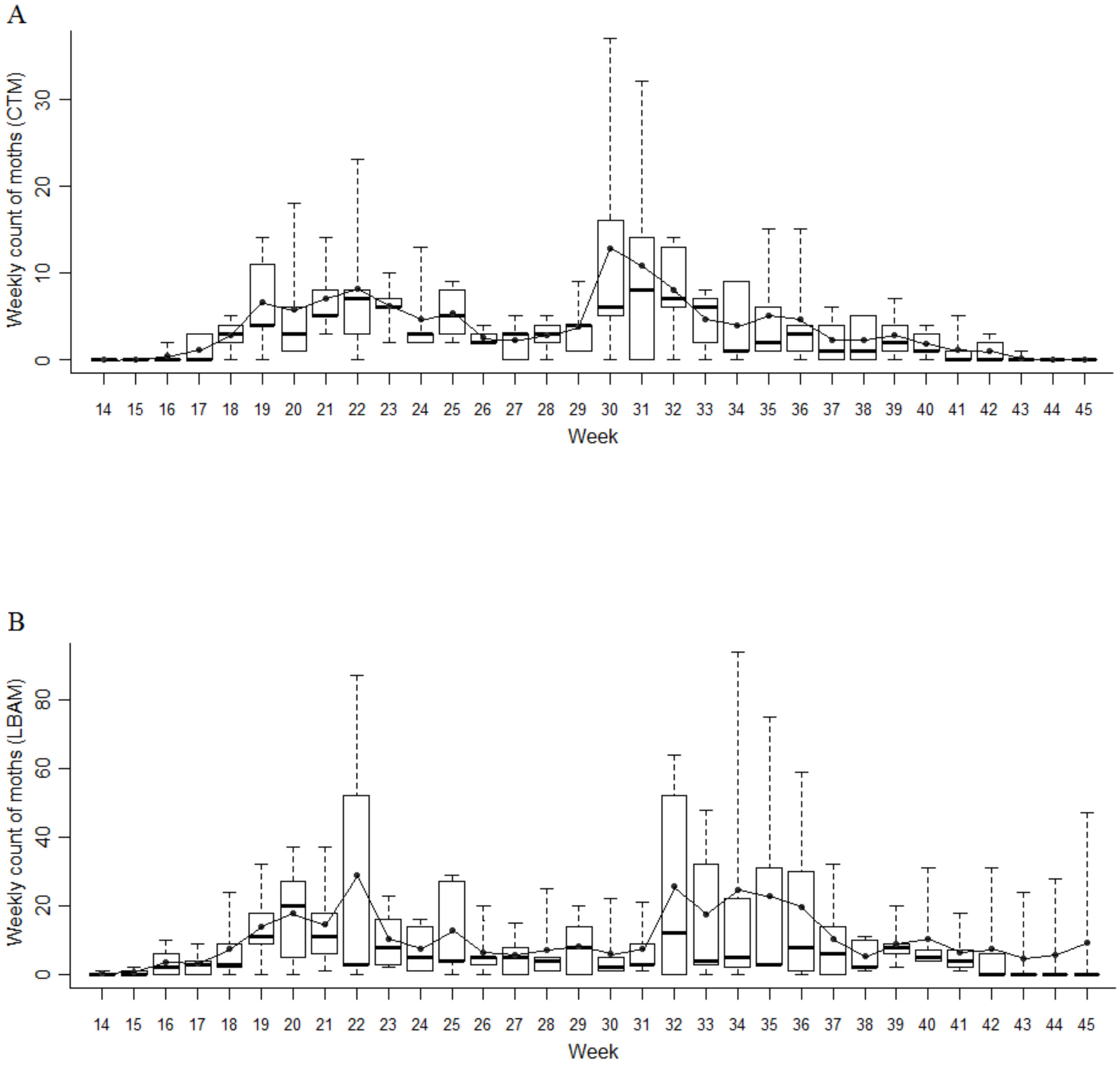


Figure 2.2. Cumulative seasonal abundance of two tortricid moth species, A – *Cacoecimorpha pronubana* (CTM), and B – *Epiphyas postvittana* (LBAM). The boxplots show the central tendency of counts per week for all years, represented by the central 50% of the data. The horizontal line in boxes shows the median, the dashed lines show the range, and the dots show the mean. The horizontal line that runs along the x-axis from week 14 to 45 across the box & whiskers connects the means representing the mean seasonal abundance of the moth for the years 2015–2019.

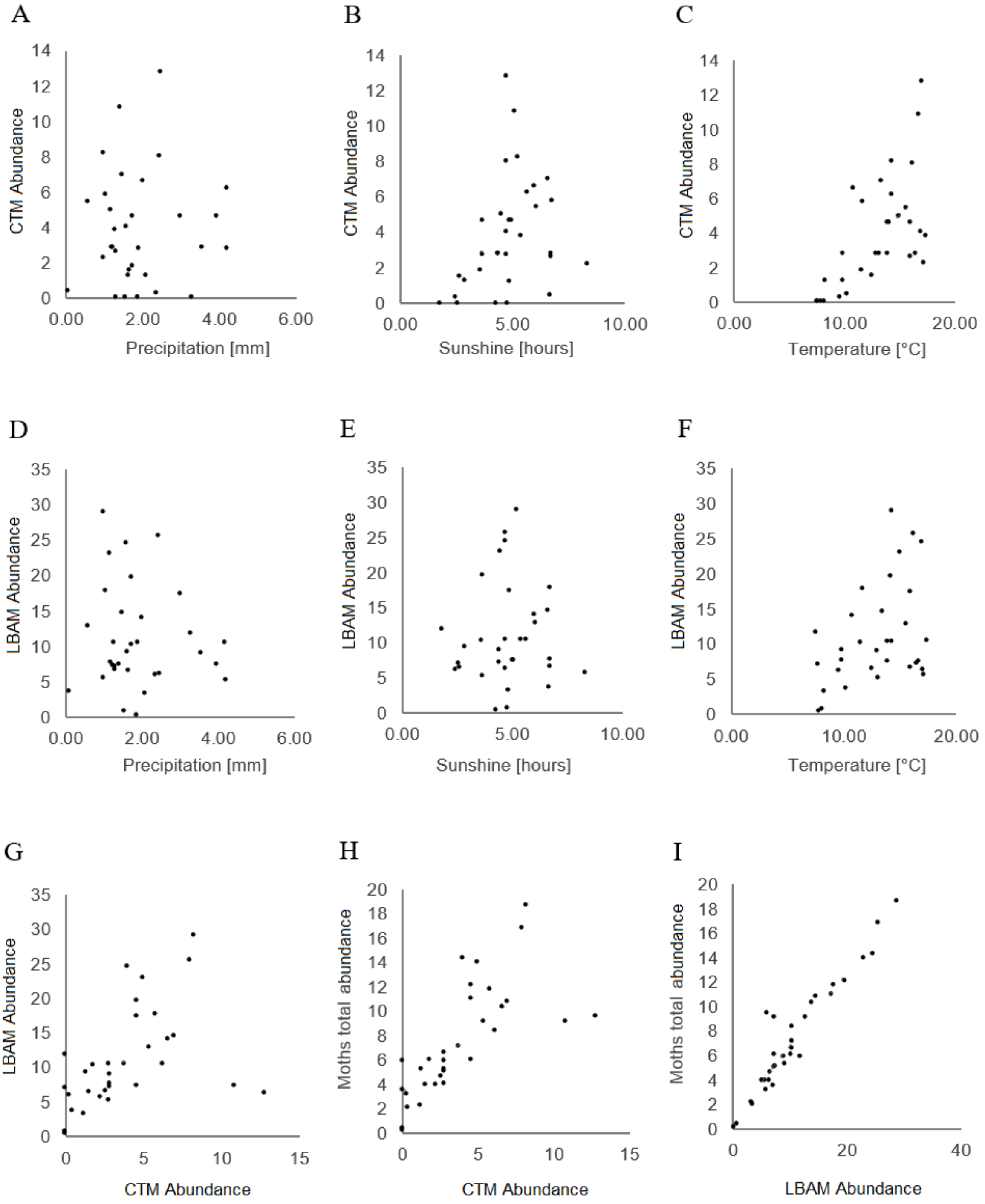


Figure 2.3. Scatter plots represent correlation between mean weekly abundance of moths, *Cacoecimorpha pronubana* (CTM) and *Epiphyas postvittana* (LBAM), and three abiotic factors represented by mean weekly precipitation (rainfall in millimetres), sunshine duration (hours) and temperature (degree Celsius) per five-year cumulative period study (2015–2019) (A–F). Figures G, H and I, show correlations of the mean abundance between both moths, and between cumulative data for both moths, and either of the moth.

2.5. Discussion

This study analysed the seasonal abundance of two herbivorous pest moth species, *C. pronubana* and *E. postvittana*, in an ornamental crop habitat over a five-year study in relation to precipitation, sunshine duration and temperature. Both species exhibited bimodal patterns of the seasonal abundance, due to their known bivoltine life history. The first generational peak was observed between May and June, week 18–25 (first generation), and the second peak around August, week 30–37 (second generation) for both species. An increase in *C. pronubana* abundance, however, tended to appear on average one or two weeks earlier than the increase of *E. postvittana* abundance, which is consistent with previous studies (Fisher, 1924; Gratwick, 2012; Fountain and Cross, 2007; Suckling and Brockerhoff, 2010). Fisher (1924) found that the first generation of *C. pronubana* emerges in spring, after a five to seven months prolonged winter larval stage, and a second generation emerges from eggs laid in the autumn. Our results, however, suggest that the second generation of *C. pronubana* begins to appear earlier than previous studies have shown, at the end of July, and they remained active through August and September exhibiting a slow and steady decline.

Significant differences in population abundance was observed between the species in our study, reflected by significantly higher numbers of *E. postvittana* adult males caught, compared with the abundance of *C. pronubana* adult males. This was consistent for both generational peaks in each season across years, with *E. postvittana* consistently exhibiting a larger increase in abundance, than *C. pronubana*. Significant differences in abundance were also observed intra-seasonally for both species. With respect to a particular year, significant differences were observed between the species only in years 2016 and 2017. It is possible, that the large increase in numbers of *E. postvittana* in 2016 and 2017 may reflected changes in abiotic factors, e.g., favourable temperatures during the development of the moth, or milder winter that occurred prior the season in which *E. postvittana* performed better than *C. pronubana*. The same changes in abiotic factors, may not, however, have benefited *C. pronubana*, where in reverse, for example, warmer periods during development may increase the sensitivity of a certain life stage that is exposed and lead to negative effects on, e.g., reproduction (Wellington, 1960; Zhang *et al.,* 2015; Boersma *et al.,* 2018).

It is also possible that changes that occurred in the local habitats may have affected the composition of the diversity or abundance of natural enemies of these two pest species, and as a result, indirectly affecting the moth species in our study differently. It was shown, for example, that variable temperatures to which the parasitic wasp, *Trichogramma* (Hymenoptera: Trichogrammatidae) is exposed during its development, significantly reduces fecundity and longevity of the wasp (Firake and Khan, 2014). It is also possible that natural enemies of *C. pronubana* are better established in the local environment than natural enemies of *E. postvittana* (Fisher, 1924; CABI, 2020). The specificity and impact of these natural enemies on each species of moth may also be important (Buxton and Talbot, 2011; Golbaghi *et al.,* 2020). While the occurrence of natural predators or diseases could explain the differences that were observed between our study species in terms of their seasonal first appearance and abundance, population trends of natural enemies would be required to confirm this.

A large amount of previous research has suggested that *E. postvittana* is a relatively abundant, cosmopolitan pest species (Buchanan, 1977; Suckling *et al.,* 1985; Burnip and Suckling, 2001; Fountain and Cross, 2007; Suckling *et al.,* 2014) with significant potential for becoming established in new habitats (He *et al.,* 2012). It is thought that local abundance from season to season is influenced by climate, larval host plants and predation (Danthanarayana; 1983). The abundance of *C. pronubana* populations, however, remains well established in known habitats (Cavalloro, 1986; Leandro *et al.,* 2002; Ostrauskas *et al.,* 2008; Brown *et al.,* 2010), but the factors that the moth is exposed to in those habitats, such as environmental pollutants (Uhl *et al.,* 2016) weather fluctuations or host plants diversity (Calvo and Molina, 2003) often govern the species own unique dynamics. Nonetheless, due to global temperature rise, *C. pronubana* also exhibits the potential to migrate into new habitats (LaštůVka, 2009).

Specific differences between years were analysed exclusively for each species, and it was found that the seasonal abundance for *C. pronubana* differed significantly between seasons throughout the five-year study period, while the seasonal abundance for *E. postvittana* did not differ significantly between these years. It is possible, that differences between years in seasonal abundance of *C. pronubana* may be characterised by inter-seasonal variations in phenological patterns reflected by the species susceptibility to certain environmental changes (e.g., weather conditions, host plant habitats). It appears, however, equally possible that *E. postvittana* populations within each season are more uniform between years, and perhaps indicates that this species is better adapted to withstand changes, recover quickly, or thrive when conditions become more suitable (Kingsolver, 1989; Kiritani, 2013; Khaliq *et al.,* 2014).

Our results also suggest that the abundance of *C. pronubana* were associated with sunshine duration and temperature, exhibiting moderate positive correlations. Carnation tortrix moths are inactive during the day, but in the early morning sun and towards dusk or summer evenings adults become active, with the male being much more active than females (Fisher, 1924). It is likely, that such activity may be correlated with the release of pheromones by female moths (Witzgall and Frérot, 1989). The phenomenon that *C. pronubana* exhibited – an increase in number of adult males appearing with an increase in temperature, is well known to occur in insects (Taylor, 1963; Solbreck, 1991; Gilbert and Raworth, 1996). None of the abiotic factors analysed here correlated with the seasonal abundance of *E. postvittana*, and seasonal abundance of neither species was correlated with rainfall.

Both species of moth tended to appear in greater numbers when the length of the mean daily sunshine duration ranged approximately between 4–6 hours per day (Figures 2B and 2E). In terms of air temperature, it was observed that the adult males from both species were only found within the temperature range of approximately 8°C and 18°C, respectively (Figures 3C and 3F). The lowest temperature threshold that was observed for *E. postvittana* was similar to other studies (Danthanarayana, 1975; Suckling and Brockerhoff, 2010). The possibility cannot be excluded, however, that abiotic factors acted on the volatility of the pheromone lures used or the mobility of the male moths, both of which may have led to differences in trap catches (Li *et al.,* 2019; Pitcairn *et al.,* 1990). Equally, temperature may have been involved in the perception of the sex pheromone through the neural pathways, and not as a result of an increase in motor activity, or in the increased release rate of the pheromones at higher temperatures (Linn *et al.,* 1988).

A moderate positive correlation was observed between the cumulative seasonal abundance of the two moth species over the five-year study period. A similar correlation was observed for *C. pronubana* when compared to the total combined seasonal abundance of both species, although, the strongest positive correlation was exhibited here by *E. postvittana* (Figure 2.3G–2.3I).

Results presented here illustrate that the seasonal abundance of these two species are similar. Significant differences, however, were observed in abundance between these two species, both within and between years. Both species of moth qualitatively exhibited two distinct generational peaks for the geographical region studied here.

Our findings from this study on phenology and abundance of these two pest species indicate that patterns measured here have a tendency to occur repeatedly from season to season, but the patterns recorded here differ from previous studies, such as the finding that the start of *C. pronubana* flight activity is earlier than has previously been reported. These results may be useful in developing local or regional forecasting models, e.g., based on phenology model proposed by Milonas and Savopoulou-Soultani (2006) in improving integrated pest management practices and in developing more efficient crop management strategies for these two species in the ornamental crop habitats.

Chapter 3. Oviposition preference of two moth species, *Cacoecimorpha pronubana* and *Epiphyas postvittana* (Lepidoptera: Tortricidae)

3.1. Abstract

The carnation tortrix moth, *Cacoecimorpha pronubana* (Roelofs and Brown, 1982), and the light brown apple moth, *Epiphyas postvittana* (Walker, 1863) (Lepidoptera: Tortricidae), are economically important pest species affecting many horticultural crops. Damage to the crop is caused by the larvae of these two polyphagous moth species. It is unclear, however, how the female oviposition behaviour may be affected by the crop plants on which the moth developed as a larva. It was hypothesised that both species of moth exhibit similar oviposition behaviour and may affect crop plants differently. Both moth species were reared exclusively on *Prunus laurocerasus* for four generations, and were allowed to oviposit on six different host plant species – *Choisya* (Rutaceae), *Euonymus* (Celastraceae), *Griselinia* (Griseliniaceae), *Photinia* (Rosaceae), *Prunus* (Rosaceae), and *Pyracantha* (Rosaceae). This study investigated the oviposition preference of two species of moth in terms of fecundity expressed by the number of eggs and the number and the size of egg clutches. The experiments were completed under controlled environmental conditions at 20°C, relative humidity of 60% and a 16L:8D photoperiod. No significant difference was observed in terms of the total number of eggs laid between *C. pronubana* and *E. postvittana* (2361 and 2546), respectively. No differences were also recorded for a clutch size between these two generalist species – mean (±SEM) of 22.08 ± 2.09 and 14.45 ± 2.52 eggs laid per clutch for *C. pronubana* and *E. postvittana*, respectively. It was observed, however, a significant difference in oviposition preference between the six host plant species; in order of preference, *C. pronubana* preferred *Griselinia* the most, following in by *Prunus, Pyracantha, Photinia, Euonymus* and *Choisya,* respectively. *Epiphyas postvittana,* however, preferred *Prunus* the most, followed by *Photinia, Pyracantha, Griselinia, Euonymus* and *Choisya*, respectively. The results from this study may help in developing more accurate strategies for biological control programmes and integrated pest management strategies within horticultural crop habitats; this through improved understanding where eggs are more likely to be laid.

3.2. Introduction

The carnation tortrix moth, *Cacoecimorpha pronubana* (Roelofs and Brown, 1982), and the light brown apple moth, *Epiphyas postvittana* (Walker, 1863) (Lepidoptera: Tortricidae), are economically important polyphagous pest species (Brown *et al.,* 2010; Suckling and Brockerhoff, 2010). Together, they affect over 500 plant species of which many are horticultural crops (Kacar and Ulusoy, 2008; Brockerhoff *et al.,* 2011; Pencheva and Yovkova, 2016; Reddy, 2016). Plant species that belong to the families Asteraceae, Fabaceae, Oleaceae, Rosaceae, Rutaceae, Solanaceae (Beitia *et al.,* 2016; CABI, 2020) and Griseliniaceae (personal observation), are those that are commonly affected by the larvae of both generalists (Fisher, 1924; Lo *et al.,* 2000). Damage to the plant is caused by the larva that produces silk and uses it to build a shelter rolling leaves together, and feeds of the foliage. As the larval mortality can reach up to 87% prior this phase, time for establishing a suitable feeding site is crucial (Fisher, 1924; Foster and Howard, 1999).

Oviposition behaviour in many species is often related to the genetic predisposition in the ability of larvae to digest certain food, yet, the suitability of a host plant for the larval development depends on several factors (Jaenike, 1978). Considering the limited food resources that neonate larvae may be initially exposed to, the right choice of a host plant for oviposition may be seen as an important factor for most Lepidopteran species (Zhang *et al.,* 2012). In theory, the choice of a host plant on which the adult female lays her eggs should be reflected by her experience as a larva that would guarantee the best possible outcome for her offspring in terms of survival, fitness and reproductive success (Awmack and Leather, 2002), however, the mechanisms by which oviposition preference is governed are more complex (Jaenike, 1978; Videla *et al.,* 2012). A good example of such complexity in oviposition behaviour is the female adult of *E. postvittana*. The female spends most of its life immobile, resting on a plant or other surfaces. The initial factor that determines her choice for oviposition, and possibly one of the most important, is the surface on which the female intends to lay her eggs, choosing smoother surfaces over uneven, irregular or hairy (Foster *et al.,* 1997; Foster and Howard, 1999). Apart from physical cues, the female also uses visual and chemical cues to choose host plants (Brockerhoff *et al.,* 2011). It was shown, for example, that the colour green, the texture of the material and the light conditions are highly important stimuli for oviposition of *Lobesia botrana* ([Denis and Schiffermüller, 1775]) and *Eupoecilia ambiguella* (Hübner, 1796) (Lepidoptera: Tortricidae) (Foster *et al.,* 1997), although, not all Tortricidae may be affected by the same stimuli equally. For example, when the preference of colours for oviposition were tested on *Amorbia* sp. Clemens, 1860 (Lepidoptera: Tortricidae) none of the colours affected the egg laying behaviour (Gutiérrez and Celestina, 2013).

Oviposition preferences in insects have been shaped as a result of evolutionary adaptations to constantly changing habitats (Jaenike, 1978; Jongsma *et al.,* 2010). In view of many attempts to explain the mechanisms upon which the oviposition preference functions, from Hopkins Host Selection principle (Hopkins, 1917), to the optimal oviposition behaviour theory (Jaenike, 1978), it appears that there is no such uniform model that would encompass the complexity of this phenomenon and determine the principles of its mechanisms (Scheirs and De Bruyn, 2002; Mader *et al.,* 2012; Karolewski *et al.,* 2017). Horticultural crops are often complex habitats that are subjected to constant changes (Son *et al.,* 2016; Van Kleunen *et al.,* 2018), which, as a result, may affect an ecological stability of a crop habitat and impose constrains on the adoption of an existent integrated pest management (IPM) strategies.

The aim of this study was to expand existing knowledge on oviposition preference and behaviour of two pest species of moth, *C. pronubana* and *E. postvittana,* and help in developing more accurate IPM strategies within horticultural crop habitats, e.g., introduction of plant species or artificial surfaces within crop habitats that would manipulate and inhibit oviposition preference of these two tortricid species. It was hypothesised that the oviposition preference of these two species of moth differs between the species of moth, and between six host plant species, or other surfaces to which these two herbivores were presented. The objective of this study was to test and measure the oviposition behaviour in terms of the number of eggs and egg clutches laid on each host plant species or artificial surfaces, and determine oviposition preference of these two tortricid species.

3.3. Materials and Methods

3.3.1. Host plants

Plant material for the experiment was obtained from an ornamental plant nursery in Shropshire, UK (52°37’20’’ N, 2°15’20’’ W; 119 m a.s.l.). The material consisted of six plant species that are commonly attacked by *C. pronubana* and *E. postvittana*; these were: the Mexican orange, *Choisya ternata* Kunth ‘Lich’ (Rutaceae), the Japanese spindle tree, *Euonymus japonicus* Thunb. var. Ovatus Aureus (Celastraceae), the New Zealand broadleaf, *Griselinia littoralis* Raoul (Griseliniaceae), the Christmas berry, *Photinia* Lindl. ‘Red Robin’ (Rosaceae), the cherry laurel, *Prunus laurocerasus* var. *schipkaensis* Späth ex H. L. Späth (Rosaceae), and the firethorn, *Pyracantha angustifolia* (Franch.) C. K. Schneid. (Rosaceae). Two years before the beginning of the experiment plants were propagated from softwood cuttings that were collected at the abovementioned ornamental plant nursery. Plant material was grown in 9-cm diameter, of 10 cm height black plastic pots filled with Sinclair® All Purpose Growing Medium Compost (Sinclair Pro, UK) under protected greenhouse conditions at the same plant nursery.

3.3.2. Insects

Two moth species – *Cacoecimorpha pronubana* and *Epiphyas postvittana* were collected in August 2018, from the same ornamental plant nursery form which the host plants were obtained. Two moth cultures were established in two separate BugDorm-4D® Insect Rearing Cages (47.5 x 47.5 x 47.5 cm) (MegaView, Taiwan) placed in a Fitotron® SGR plant growth room (Weiss Technik, UK) maintained at a constant temperature 20°C, 60% RH and 16L:8D photoperiod. Moths were reared on a mixture of six abovementioned host plants for twelve months. From July 2019 moths were reared exclusively on *Prunus laurocerasus* var. *schipkaensis* Späth ex H. L. Späth (Rosaceae). Cultures were maintained for twelve months up to the beginning of the experiment.

3.3.3. Experiments

The experiment was set up in August 2020 in a Fitotron® SGR 'Walk-in' plant growth room under the same controlled environmental conditions used to maintain the cultures of *C. pronubana* and *E. postvittana*. Two BugDorm-4D® Insect Rearing Cages (47.5 x 47.5 x 47.5 cm) (MegaView, Taiwan) were used, one cage for each of the two species of moth. The experiment was replicated three times. Six host plant species were placed in the centre of inside each cage – *Choisya, Euonymus, Griselinia, Photinia, Prunus, Pyracantha*. Plants were arranged in a circle alongside the outer side of the perimeter of the circle of 20 cm diameter, maintaining uniform distance between plants. The height and the mid-width of the plants was approximately 20 cm, and 12 cm, respectively. The plants were allowed to touch each other, but not obscure one another.

Pupae were transferred separately to Petri dishes (90 mm diameter x 15 mm height), and placed undisturbed in the same room under the same constant environmental conditions. Each Petri dish had a circular piece of dry plain white paper towel placed on the bottom of the dish.

At the beginning of the experiment the following procedures were applied for each species of moth: after eclosion, four unmated adult females and four unmated adult males (all moths approximately 24h old) of the same species of moth were randomly selected from the pupae collected prior the experiment, and placed together in one Petri dish. The dish was then placed inside the cage with six host plants in the centre of the 20 cm circle, 10 cm above the bottom of the cage. The top of the Petri dish was then removed allowing adult moths to disperse.

Adult females were allowed to lay eggs up to ten days or until their death. After the oviposition was completed each plant, pots and the cage inside were inspected and number of clutches and eggs per each clutch recorded on all surfaces using a hand lens (21 mm diameter, 30x magnification), or a Microtec HM-3® stereo microscope.

3.3.4. Statistical analyses

All statistical tests were performed using R version 4.0.2 (R Core Team, 2020), and the significance level was set at $\alpha=0.05$. The analyses were used to measure the effect of six host plant species on the oviposition preference, as well as fecundity of two moth species. Fecundity was defined by the total number of eggs laid, as well as, the size of clutches (the number of eggs per clutch). Oviposition preference, in terms of fecundity, was compared between the moths and the host plants for each species of moth. One-way analysis of variance (ANOVA) was used to compare means of clutch sizes, and evaluate their association between the two species of moth using Pearson’s correlation. Chi-squared goodness of fit test for given probabilities was used to compare the observed distribution to an expected distribution of the number of eggs laid between host plants species and artificial surfaces on which moth deposited their eggs. When data did not meet normality (Shapiro-Wilk test) or homogeneity of variances assumptions (Levene’s test), non-parametric Unpaired Two-Samples Wilcoxon test was used (Mann-Whitney test) to compare an overall fecundity between the two moth species, with further analyses performed with the Kruskal-Wallis test to compare the differences between the six host plant species and artificial surfaces on which moth deposited their eggs. Wilcoxon test was used for *post hoc* pairwise comparisons (with P-values adjusted by Benjamini and Hochberg (BH) method).

3.4. Results

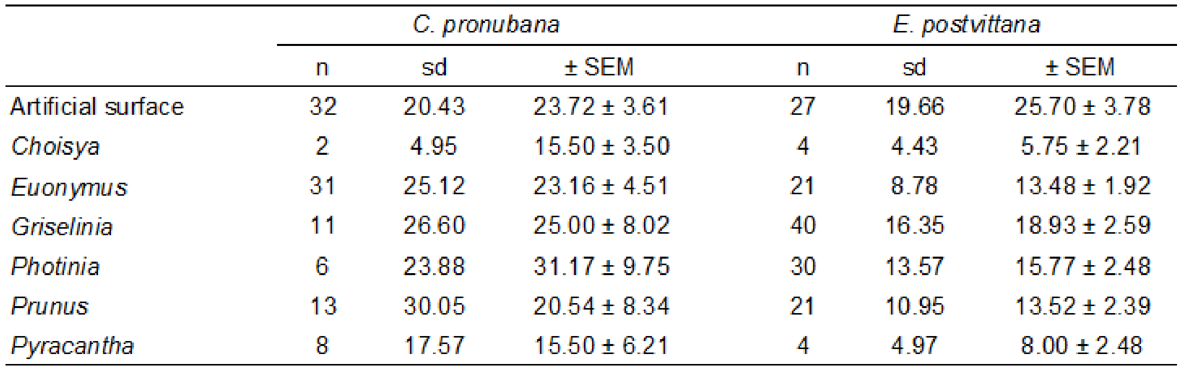
Apart from artificial surfaces (plastic), eggs were typically laid on the upper surface of the leaves of the host plants, although, some eggs were found on the underside of the leaves. This phenomenon was supported by other studies (Burges and Jarrett, 1976; Foster *et al.,* 1997).

The eggs were laid in separate clutches or as a single egg, clutches contained between 1 – 121 eggs for *C. pronubana*, and 1 – 69 eggs for *E. postvittana.* With regard to the surface or a host pant on which moths deposited eggs, the mean maximum and the mean minimum number of eggs laid per clutch from each replicate was (±SEM) 74.71 ± 11.82 and 3.86 ± 1.44, respectively for *C. pronubana*, and 43.14 ± 9.99 and 1.57 ± 0.43, respectively for *E. postvittana.* There were no significant differences observed between the mean maximum clutch size between the two moth species (One-way ANOVA: F =

4.16, df =1, P = 0.064), and the mean minimum clutch size (One-way ANOVA: F = 2.32, df =1, P = 0.154).

The total number of eggs laid for *C. pronubana* and *E. postvittana* was 2361 and 2546, respectively, showing no significant difference between the two moth species (Wilcoxon rank sum test: W = 22, P = 0.798). Similarly, fecundity in terms of the mean number of eggs deposited per clutch (clutch size) did not show any significant differences between *C. pronubana* and *E. postvittana* (Wilcoxon rank sum test: W = 8278, P = 0.209) (Figure 3.1). With the total mean (±SEM) of 22.08 ± 2.09 and 14.45 ± 2.52 eggs laid per clutch for *C. pronubana* and *E. postvittana*, respectively (Table 3.1), there was a significant difference between the means of clutch size between the two moths (One-way ANOVA: F = 5.42, df = 1, P = 0.038), however, there was no significant correlation observed between the means of clutch sizes between the moth species (Pearson's product-moment correlation: t = 1.898, df = 5, P = 0.116, r = 0.65).

Table 3.1. Mean number of eggs deposited per clutch per each host plant species (clutch size) (± SEM) for two species of moth, *C. pronubana* and *E, postvittana* (sd – standard deviation, n – number of clutches deposited).



	C. pronubana			*E. postvittana*		
	n	sd	± SEM	n	sd	± SEM
Artificial surface	32	20.43	23.72 ± 3.61	27	19.66	25.70 ± 3.78
Choisya	2	4.95	15.50 ± 3.50	4	4.43	5.75 ± 2.21
Euonymus	31	25.12	23.16 ± 4.51	21	8.78	13.48 ± 1.92
Griselinia	11	26.60	25.00 ± 8.02	40	16.35	18.93 ± 2.59
Photinia	6	23.88	31.17 ± 9.75	30	13.57	15.77 ± 2.48
Prunus	13	30.05	20.54 ± 8.34	21	10.95	13.52 ± 2.39
Pyracantha	8	17.57	15.50 ± 6.21	4	4.97	8.00 ± 2.48

Cacoecimorpha pronubana adult females laid on average 63 (32.1%), 3 (1.3%), 60 (30.4%), 23 (11.6%), 16 (7.9%), 22 (11.3%) and 10 (5.3%) eggs on the artificial surface, on *Choisya, Griselinia, Prunus, Photinia, Pyracantha* and *Euonymus*, respectively. *Epiphyas postvittana*, however, laid 58 (27.3%), 2 (0.9%), 24 (11.1%), 63 (29.7%), 39 (18.6%), 24 (11.2%) and 3 (1.3%) eggs on the artificial surface, on *Choisya, Griselinia, Prunus, Photinia, Pyracantha* and *Euonymus*, respectively. Fecundity in terms of the mean number of eggs laid per female between host plant species and other surfaces on which eggs were laid was significantly different for both, for *C. pronubana* (Chi-squared: X^2 = 120.91, df = 6, P < 0.0001) and for *E. postvittana* (Chi-squared: X^2 = 116.26, df = 6, P < 0.0001). The mean number of eggs laid for *C. pronubana* and *E. postvittana* was 196.75 ± 9.03 and 212.17 ± 9.23, respectively, which complies with other studies (Fisher, 1924; Suckling and Brockerhoff, 2010). There was no significant difference, however, in fecundity in terms of a clutch size between six host plant species or surfaces for both species of moth, *C. pronubana* (Kruskal-Wallis: $X^2 = 6.67$, $P = 0.352$), and *E. postvittana* (Kruskal-Wallis: $X^2 = 10.96$, $P = 0.09$); neither there was a difference in any of the pairs compared using Wilcoxon rank sum test with continuity correction (P-value adjusted by BH) (Figure 3.2 and Table 3.1).

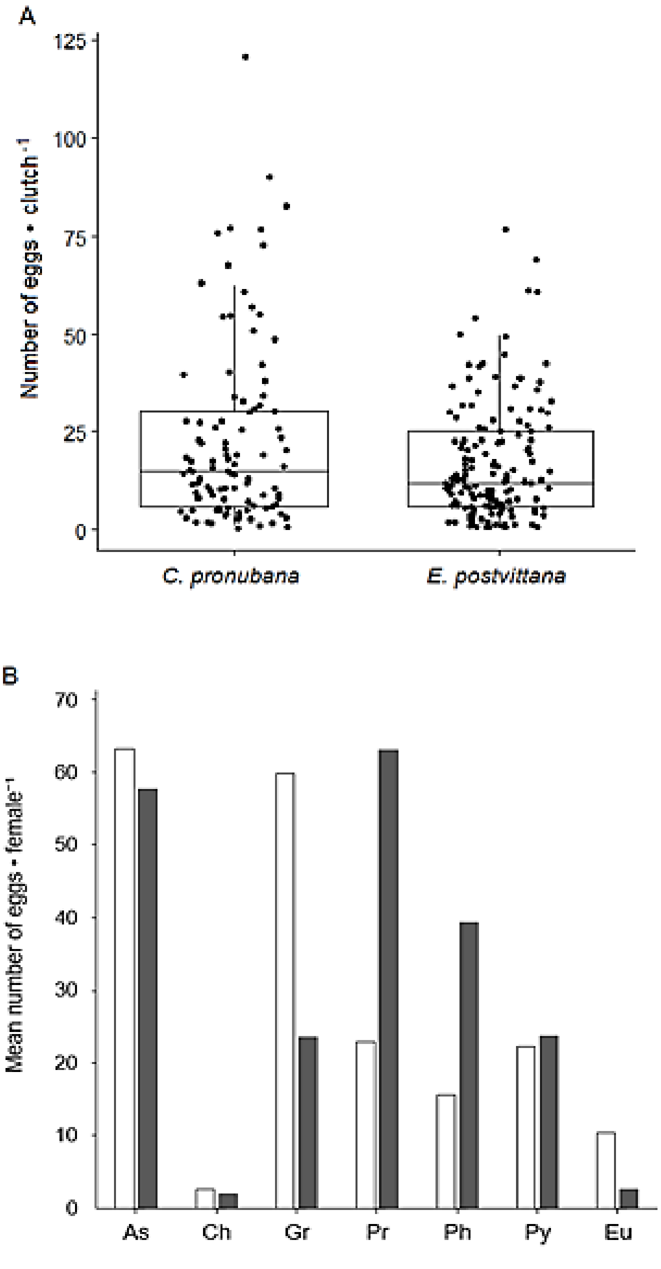
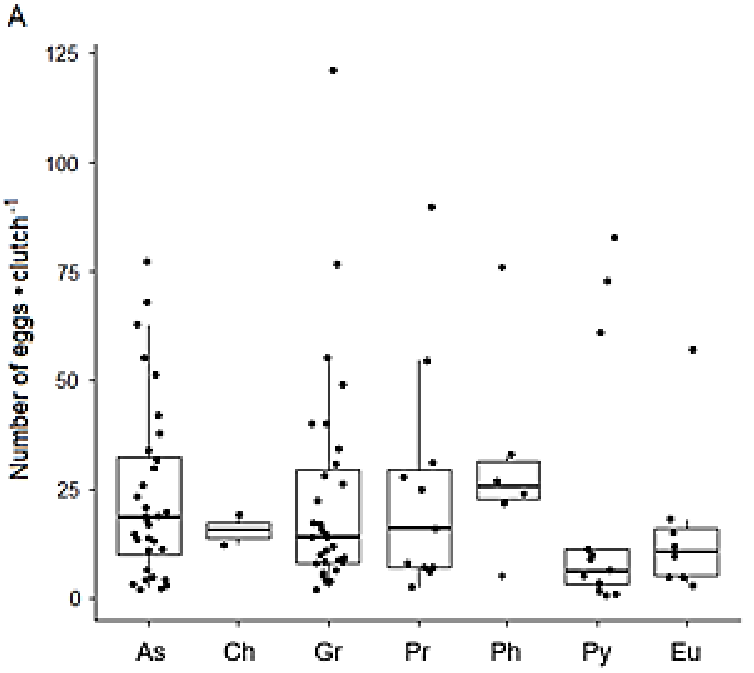


Figure 3.1. Comparison of fecundity between two species of moth – *C. pronubana* and *E. postvittana*; A – between two species of moth in terms of a clutch size, represented in the number of eggs laid per clutch. Black dots represent data points, each representing a clutch; scattered data points for each moth species were intentionally horizontally spread in order to avoid the points being obscured by each other. B – between *C. pronubana* (white bars) and *E. postvittana* (dark grey bars) in terms of the mean number of eggs oviposited per female on six different host plants (Ch – *Choisya*, Gr – *Griselinia*, Pr – *Prunus*, Ph – *Photinia*, Py – *Pyracantha*, Eu – *Euonymus*) and on artificial surface (As).



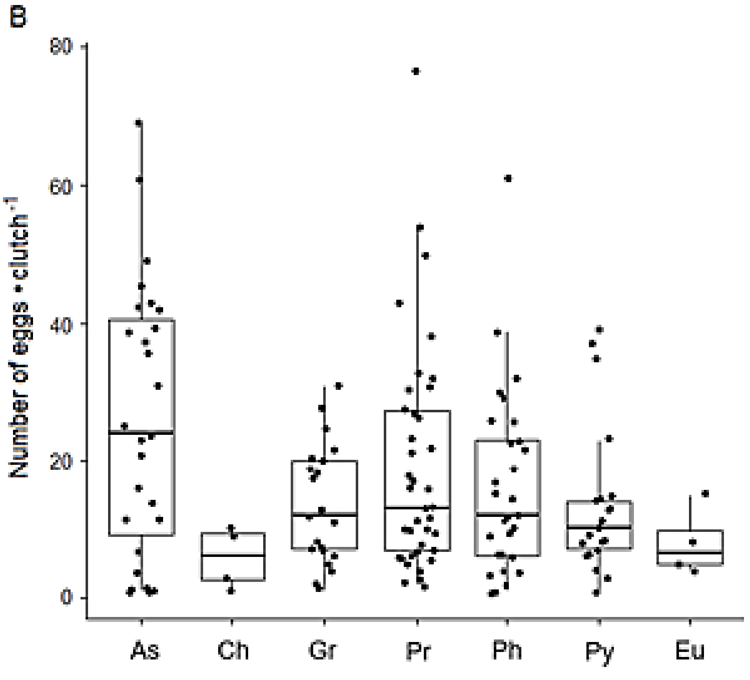


Figure 3.2. Comparison between the total fecundity in terms of a clutch size between six host plant species or artificial surface on which moth deposited eggs, for *C. pronubana* – A, and *E. postvittana* – B, (As – artificial surface, Ch – *Choisya*, Gr – *Griselinia*, Pr – *Prunus*, Ph – *Photinia*, Py – *Pyracantha*, Eu – *Euonymus*). Clutch size is represented in the number of eggs laid per clutch. Black dots represent data points, each representing a clutch.

3.5. Discussion

This study demonstrates the effect of host plants on oviposition preference of adult females of *C. pronubana* and *E. postvittana* reared exclusively on *Prunus* diet prior the experiment. Oviposition preference was determined by the fecundity in terms of the total number of eggs laid by the adult female of ether of the moth species, and by the clutch size, which was defined by the number of eggs deposited per clutch.

The moths laid their eggs on host plants and on artificial surfaces. Egg deposition on surfaces other than plants is a common phenomenon that is observed for both of these herbivore species (Fisher, 1924; Burges and Jarrett, 1976; Foster and Howard, 1999). Neither of the two moths studied here showed a significant difference in fecundity in terms of a clutch size between the six host plants or other surfaces. There were also no significant differences in the clutch size observed between these two insect species. Consequently, in terms of a clutch size, no tendency was observed in oviposition preference or an aversion to *Prunus* from which both moth species originated, or to any other rosaceous hosts.

A significant difference, however, was noticed in the proportion of the mean number of eggs laid per female between the host plants and other artificial surfaces on which moth of either species preferred to deposit its eggs. On average, *C. pronubana* laid a similar number of eggs on the artificial surface as on *Griselinia*, which was significantly proportionally more than on any of the other hosts to which the moth was exposed. Similarly, the oviposition preference for *E. postvittana* on the same artificial surface, but – on the contrary to *C. pronubana*, with a preference to oviposit on *Prunus*. Apart from equal interests in depositing eggs on artificial surface, it appears that *C. pronubana* preferred *Griselinia*, and *E. postvittana* preferred *Prunus* when choosing the host plant on which to oviposit. It appears that the larval food plant did affect oviposition preference of these two generalists differently, although, the oviposition preference of *C. pronubana* may contradict the Hopkins Host Selection Principle, as the moth did not reflect its experience as a larva developing on *Prunus* (Hopkins, 1917; Barron, 2001). It is possible, however, that the oviposition decisions were governed by a learned-behaviour of a female subjected to trade-offs that relates to enemy-free habitat for eggs and offspring, as well as to offspring performance (Roitberg *et al.,* 1999; Videla *et al.,* 2012; Zhang *et al.,* 2012.). It is unclear, however, why the oviposition preferences included significant amount of eggs laid on artificial surface.

It is well-documented that plant volatile compounds are important olfactory cues affecting oviposition behaviour in Lepidopterans (Leather, 1995; Witzgall *et al.,* 2005. Markheiser *et al.,* 2020). Chemical signals generated by plants often carry information about plant quality, such as plant age, growth rate, nutritional status or damage caused by herbivorous insects (Awmack and Leather, 2002; McCallum *et al.,* 2011). It was shown, for example, that isothiocyanates (iberin and sulforaphane) can stimulate oviposition behaviour of the diamondback moth, *Plutella xylostella* (Linnaeus, 1758) (Lepidoptera: Plutellidae) (Renwick *et al.,* 2006), whereas the pine beauty moth, *Panolis flammea* (Denis and Schiffermüller, 1775) (Lepidoptera: Noctuidae) oviposition can be stimulated by pine monoterpenes (Leather, 1987). Oviposition behaviour of the female moth can consequently manifest itself in the preference to oviposit on the older parts of host plants than on the younger, e.g., the western spruce budworm, *Choristoneura freemani* Razowski, 2008 (Lepidoptera: Tortricidae), the smaller tea tortrix, *Adoxophyes honmai* Yasuda, 1998 (Lepidoptera: Tortricidae), or the carnation tortrix moth, *C. pronubana*, (Burges and Jarrett, 1976; Leyva *et al.,* 2000; Piyasaengthong *et al.,* 2016). A similar tendency was seen for *C. pronubana* and *E. postvittana* in this study.

It is possible that oviposition preference of *C. pronubana* and *E. postvittana* in this study was not solely governed by the chemical properties of the plants, but rather the physical characteristics of the surface on which eggs were deposited (Hagley *et al.,* 1980; Tomkins *et al.,* 1991). Foster *et al*. (1997) showed that surface texture is an important factor determining the oviposition behaviour of the adult female of *E. postvittana.* They found that female prefers to lay her eggs on smoother surfaces rather than on the rougher (Foster *et al.,* 1997). Burges and Jarrett (1976), showed similar oviposition behaviour for *C. pronubana* in glasshouse conditions indicating that the adult female moths laid proportionally four and a half times more eggs on glass and wooden structures than on a plant foliage (Burges and Jarrett, 1976).

The model on the optimal oviposition behaviour theory predicts that female choice of a host plant (or other surface) on which to oviposit may be constrained by the available time within which female may also choose to search for more suitable host (Jaenike, 1978). Foster *et al*. (1997), however, showed that it is not the amount of landing or a time spent on the surface of interest, but the rise wax ridge on a smooth surface that may influence the oviposition behaviour of *E. postvittana* (Foster *et al.,* 1997). A similar relationship was shown also for *C. pomonella* (Linnaeus, 1758) on different fruit and leaf surfaces (Hagley *et al.,* 1980). Rid *et al*. (2018), however, showed that oleanolic acid naturally occurring in the cuticular wax may be the key chemical cue that determines the oviposition acceptance behaviour of the vine moth, *Eupoecilia ambiguella* (Hübner, 1796) and the European grapevine moth, *L. botrana* ([Denis and Schiffermüller, 1775]) (Lepidoptera: Tortricidae) (Rid *et al.,* 2018).

Apart from physical or chemical stimuli, moths can also use visual cues to choose the oviposition site (Brockerhoff *et al.,* 2011), such as colour or foliage structure (Foster *et al.,* 1997). Perhaps, foliage density may have contributed to the factors that affected oviposition preference of *C. pronubana* and *E. postvittana* in this study. As the foliage structure or an array of leaves were not an objective of this study, it is worth a note that other authors observed that denser foliage tends to encourage the moth to oviposit more eggs, for example, the adult female of *E. postvittana* (Foster *et al.,* 1997; Wearing, 1998).

This study illustrates that females of these two moth species display characteristic oviposition behaviour known to polyphagous insects (Jaenike, 1978). Considering that both moths laid a significant number of eggs also on the artificial surface, it is possible that the moths were influenced by the mixture of both physical and chemical characteristics of the surfaces on which they deposited eggs. Perhaps females can recognise the limited choice in oviposition they have, or the scarcity of the host plant availability, and try to broaden the range of ‘possible plant species’ on which to deposit eggs potentially increasing the survival of the species (Thiery and Moreau, 2005). The oviposition behaviour that was observed in this study may also reflect species genetic predisposition in ability to accept sudden dietary changes (as both species originated from *Prunus* diet regime). It is possible that under such conditions an individual female moth may choose to deposit eggs on alternative plant species simultaneously increasing the variety of utilised host species (Jaenike, 1978). Such circumstances may be advantageous for these species creating an opportunity for their dispersal and distributions within its habitats and beyond (Thompson and Pellmyr, 1991; West and Cunningham, 2002)

It is demonstrated that the oviposition preference in terms of a clutch size does not differ between *C. pronubana* and *E. postvittana*, but it differs in terms of the mean clutch size laid on six host plant species. It was also showed that the mean number of eggs laid per female per host plant species or artificial surface significantly differed between host plant species/surfaces for both species of moth. The results presented here for these two generalist species of moth may be helpful in developing integrated pest management systems within ornamental crop habitats. For example, understanding where eggs are more likely to be laid (e.g., artificial surfaces or particular host plants when combination of plant species are grown within an ornamental nursery) may help to focus monitoring and control efforts as part of an IPM programme. As such, it is hoped that this work will prompt further work in this area.

Chapter 4. Effect of host plant on the life history of the carnation tortrix moth *Cacoecimorpha pronubana* (Lepidoptera: Tortricidae).

4.1. Abstract

The carnation tortrix moth, *Cacoecimorpha pronubana* (Hübner, [1799]) (Lepidoptera: Tortricidae), is one of the most economically important insect species affecting the horticultural industry in the UK. The larvae consume foliage, flowers or fruits, and/or rolls leaves together with silken threads, negatively affecting the growth and/or aesthetics of the crop. In order to understand the polyphagous behaviour of this species within an ornamental crop habitat, it was hypothesised that different host plant species affect its life history traits differently. This study investigated the effects of the host plant species on larval and pupal durations and sizes, and fecundity (the number of eggs and the number and size of egg clutches). At 20°C, 60% RH and a 16L:8D photoperiod larvae developed 10, 14, 20 and 36 days faster when reared on Christmas berry, *Photinia* (Rosaceae), than on cherry laurel, *Prunus laurocerasus* (Rosaceae), New Zealand broadleaf, *Griselinia littoralis* (Griseliniaceae), Mexican orange, *Choisya ternata* (Rutaceae), and firethorn, *Pyracantha angustifolia* (Rosaceae), respectively. Female pupae were 23.8 mg heavier than male pupae, and pupal weight was significantly correlated with the duration of larval development. The lowest and the highest mean numbers of eggs were produced by females reared on *Pyracantha* (41) and *Photinia* (202), respectively. Clutch size differed significantly among moths reared on different host plants, although the total number of eggs did not differ. This study showed that different ornamental host plants affect the development of *C. pronubana* differently. Improved understanding of the influence of host plant on the moth's life history parameters measured here will help in determining the economic impact that this species may have within the ornamental plant production environment, and may be used in developing more accurate crop protection methodologies within integrated pest management of this insect.

4.2. Introduction

The carnation tortrix moth, *Cacoecimorpha pronubana* (Lepidoptera: Tortricidae) (Roelofs and Brown, 1982) is an economically important multivoltine polyphagous pest species affecting over 138 plant genera (Kacar and Ulusoy, 2008; Pencheva and Yovkova, 2016; Reddy, 2016). Damage is caused by the larva, which feeds mainly on the foliage. It spins a shelter of silk on the upper or lower surface of leaves, or ties the leaves together, and feeds between the leaf surfaces (Fisher, 1924; Bestagno, 1955). In ornamental plant production, the moth affects mainly plants in the families Aceraceae, Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Ericaceae, Fabaceae, Geraniaceae, Oleaceae, Rutaceae, Rosaceae, Salicaceae, Solanaceae (EPPO, 2020; Beitia *et al.,* 2016). It naturally occurs in the Mediterranean area, but has been present in Britain since at least 1905 (Fisher, 1924; EPPO, 2020).

While different methods have been used to control *C. pronubana*, the use of synthetic pesticides remains the most frequently used approach (Solomon *et al.,* 2001; Rehman *et al.,* 2014; Wang *et al.,* 2014). This is despite the fact that insecticides, such as neonicotinoids, pyrethroids, organophosphates and carbamates, are known, to be harmful to natural enemies of this pest, such as *Trichogramma evanescens* Westwood, 1833, a parasitic wasp of lepidopteran eggs (Wang *et al.,* 2014). In addition, pyrethroid and neonicotinoid insecticides are harmful to pollinators such as the European honey bee, *Apis mellifera* Linnaeus, 1758, and the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius, 1787) (Whitehorn *et al.,* 2017; Piccolomini *et al.,* 2018).

Although most agricultural production relies on the use of synthetic chemical pesticides to maintain high crop yields (Margni *et al.,* 2002), integrated pest management (IPM) systems have become one of the most extensively researched methods of sustainable crop production (Stenberg, 2017). IPM systems are typically based on crop monitoring, use of economic thresholds, manipulation of biotic and abiotic factors to prevent pest problems wherever possible, and where required, the application of bio-pesticides or natural enemies (Gross and Gündermann, 2016; Lamichhane *et al.,* 2016; Lemes *et al.,* 2017; Ramsden *et al.,* 2017; Rodrigues *et al.,* 2017). Host plant suitability plays an important role in shaping the feeding behaviour of a larva, and determining the larval and adult performance in terms of its longevity, body size, fecundity and mating and ovipositional behaviour (Brewer *et al.,* 1985; Lance, 2012; Moreau *et al.,* 2017). Even where an insect herbivore is polyphagous, individuals may still display improved performance on one specific host plant, family or order, in terms of reproductive success and population growth (Lance, 2012).

Little is known about the influence of the host plant species on the performance of *C. pronubana*, and how the components of its life stage correlate with each other. Knowledge of whether host plant influences performance of this pest would inform whether or not crop protection approaches should be tailored to specific crops (Bell *et al.,* 2005). Improved understanding of the life history of *C. pronubana* may also allow for the development of models of fitness for this species that can be used to predict the reproductive success of this moth within a specific crop environment, for example, and further determine the economic impact that this species may have and could be used in the development of improved pest management of this insect. Similar relationships have previously been studied, for example, for the diamondback moth, *Plutella xylostella* (Linnaeus, 1758)

(Verkerk and Wright, 1996) and the maize weevil, *Sitophilus zeamais* (Motschulsky), 1855, (Ojo and Omoloye, 2016), and used to explain observed plasticity in life-history traits (Nylin and Gotthard, 1998).

The aim of this study was to investigate the effect of the host plant on the larval development of *C. pronubana*, and the relationships between the larval stage duration and the weight of pupa of the insect. Improved understanding of larval development on different ornamental host plant species and how this affects further the moth development may be used to determine crop specific population dynamics of the moth, and management of crop infestations more effectively within an IPM system.

4.3. Materials and Methods

4.3.1. Host Plants

Six, economically important plant species that are commonly attacked by *C. pronubana* were obtained for the experiment from an ornamental plant nursery in Shropshire, UK (52°37’20’’ N, 2°15’20’’ W; 119 m a.s.l.). These were: Mexican orange, *Choisya ternata* Kunth ‘Lich’ (Rutaceae), Japanese spindle tree*, Euonymus japonicus* Thunb. var. *Ovatus Aureus* (Celastraceae), New Zealand broadleaf*, Griselinia littoralis* Raoul (Griseliniaceae), Christmas berry, *Photinia* Lindl. ‘Red Robin’ (Rosaceae), cherry laurel, *Prunus laurocerasus* var. *schipkaensis* Späth ex H. L. Späth (Rosaceae), and firethorn, *Pyracantha angustifolia* (Franch.) C. K. Schneid. (Rosaceae). Plants were propagated from softwood cuttings two years before the experiment. Cuttings were collected, propagated and grown in 9-cm diameter black plastic pots filled with Sinclair® All Purpose Growing Medium Compost (Sinclair Pro, UK) under protected glasshouse conditions at the same ornamental plant nursery. At the time of the experiment, plant’s height ranged from 20 to 25 cm, and their mid-width measured approximately 12 cm.

4.3.2. Insects

Cultures of *C. pronubana* were established using adult moths caught between April and May 2018 at the same ornamental plant nursery in Shropshire, UK, from which the plants were obtained. The moth culture was established in a BugDorm-4D® Insect Rearing Cage (47.5 x 47.5 x 47.5 cm) (MegaView, Taiwan) placed in a Fitotron® SGR plant growth room (Weiss Technik, UK) maintained at a constant temperature 20°C, 60% RH and 16L:8D photoperiod. Moths were reared on a mix of ornamental plants belonging to Caprifoliaceae, Hypericaceae, Pittosporaceae, Plantaginaceae and Rhamnaceae. Plant species and plant families that are commonly affected by the pest were carefully selected for rearing the moth culture to mimic diverse range of plants grown within an ornamental nursery and to ensure fitness of the moths used in the experiment (Merz, 1959; Freeland, 1975; Hägele and Rowell-Rahier, 1999). Plants were grown and sourced from the same ornamental plant nursery, from which the host plants were obtained. The moth colony was maintained from May to November 2018. No additional individuals were introduced after the initial establishment and during the maintenance of the culture. Second-generation neonates (0–34h old) were collected for the experiment.

4.3.3. Experiments

The experiment was conducted in a Fitotron® SGR 'Walk-in' plant growth room under the same controlled environmental conditions used to maintain the culture of *C. pronubana*. The treatments consisted of the six host plants – *Choisya*, *Euonymus, Griselinia*, *Photinia*, *Prunus* and *Pyracantha*. Each replicate consisted of a single plant and six replicates were laid out using a Latin Square design (Fisher, 1925). Plants were stood on a black PVC tray and were watered as required from beneath. Five neonates collected from the culture were placed at the same time on each plant using a fine paintbrush, after which each plant was covered with a nylon mesh sleeve (43 cm long by 13 cm diameter; mesh aperture area = 1.6×10^{-5} metre, with the open area of a mesh (A^o) = 50%) closed at the top and the bottom. Time of application was recorded for each host plant. Pupae were transferred separately to Petri dishes (90 mm diameter x 15 mm height), and placed in the same room under the same constant environmental conditions. Each Petri dish had a circular piece of dry plain white paper towel placed on the bottom of the dish. The following data were recorded for each individual moth: the cumulative duration of larval stage from neonate to pupa; the weight of pupa after the integument hardened and turned brown; as well as the date of emergence, sex and weight of adult. The adult measurements were taken between 6–12 hours after eclosion. Sex was determined using a Microtec HM-3® stereo microscope (TEC Microscopes, UK).

After eclosion and measurements one male and up to three female moths were placed into one clear Petri dish (all from the same host plant species) and were allowed to mate. Females were allowed to lay eggs on the inside walls of the dish until their death. Only the total number of eggs laid per host plant species, and the total number of egg clutches per host plant species was recorded. The females were allowed to lay eggs up to their death; during this period eggs were counted every 48h using a Microtec HM-3® stereo microscope.

4.3.4. Statistical Analysis

Statistical analyses were performed with R version 3.6.1 (R Core Team, 2020), at $\alpha=0.05$. Larval survivorship (numbers survived to pupal stage/number introduced) was compared between six host plant species, and pupal survivorship between five host plant species (analyses did not include *Euonymus*) using Kruskal-Wallis test, and *post hoc* pairwise comparisons (with P-values adjusted by Benjamini and Hochberg (BH) method) were performed with Wilcoxon test. One-way analysis of variance (ANOVA) was used to detect differences between the duration of the larval or pupal stage across the host plant treatments. Wilcoxon signed rank test with continuity correction was used to test the difference between the total number of larvae applied initially and the larvae survived, as well as between the pupae that was collected and the pupae that survived. Pupal weight was compared between six host plant species using Kruskal-Wallis test, and *post hoc* pairwise comparisons was tested using Wilcoxon test with P-value adjusted by BH method.

Correlation between duration of larval stage and pupal weight between sexes on different host plant species, its strength and the direction was tested with Pearson product-moment correlation coefficient (PPMCC). When the data were not normally distributed the Kendall rank correlation coefficient (tau) test was used to estimate a rank-based measure of association. When the correlation was significant ($P < 0.05$), the R-squared was used to indicate the strength of predictive accuracy. When the host plant species did not affect the sexes, the data were pooled from all host plants in order to analyse the correlation between the overall duration of larval stage and the overall pupal weight between sexes. The duration of larval stage and the weight of pupa between males and females was compared using non-parametric unpaired two-samples Wilcoxon test.

Fn n ecundity on different host plants was determined by the mean number of eggs laid inside Petri dishes as well as the number of eggs per clutch laid. In order to determine the differences between the mean fecundity of moths that had developed on the five different host plants, the observed numbers of eggs laid were compared with the expected values based on an equal distribution of eggs laid by adults from the five different host plants. The null hypothesis was that there is no significant difference between the observed and the expected values, and it was tested with Pearson's chi-square goodness of fit test. Kruskal-Wallis rank sum test was used to test the differences between the number of eggs laid per clutch between five different host plants, and the differences between the groups of host plants with pairwise comparisons using Wilcoxon test with P-value adjusted by BH method

4.4. Results

4.4.1. Larval and pupal survivorship

Larval survivorship was determined by pupae collected from five different host plant species - *Choisya*, *Euonymus, Griselinia, Photinia*, *Prunus* and *Pyracantha*. Survival rates differed significantly between host plant species for larvae (Kruskal-Wallis (KW): χ^2 =

26.06, df = 5, $P < 0.0001$), and for pupae (KW: $\chi^2 = 13.28$, df = 4, P = 0.009). Multiple pairwise-comparisons indicated significant differences in larval survivorship between eight pairs of host plants ($P < 0.05$) (Table 4.1).

The difference between the total number of neonate larvae placed on each plant at the start of the experiment, and the numbers of larvae that survived was statistically significant (Wilcoxon signed rank test with continuity correction (WRS): V = 406, $P < 0.0001$), and there was no difference between the numbers of pupae collected, and the numbers of pupae that survived (WRS: V = 10, P = 0.072). It was concluded that the median number of the larvae placed on each plant at the start of the experiment was significantly different from the median number of larvae that survived, however, the median number of pupae collected was not significantly different from the median number of pupae that survived.

4.4.2. Duration of larval and pupal stage

The mean duration of the larval stage (± 0.82 days; deviation of ± 1.50% from the mean) was (mean ± SEM) 54.54 ± 1.50, and pupal stage was 10.00 ± 0.30 days. Host plant species had a significant effect on larval duration (One-way ANOVA: df = 4, F = 41.6, $P < 0.0001$), but not on the duration of pupal stage (KW: $\chi^2 = 5.83$, df = 4, P = 0.212; Figure 1B). Tukey pairwise comparison indicated that the duration of larval stage between host plants differed significantly except between *Griselinia* and *Prunus,* and *Griselinia* and *Choisya* (Figure 4.1A).

4.4.3. Correlation between duration of larval stage and pupal weight between sexes

Overall, the weights of pupae collected from five different host plant species significantly differed between the plant species (KW: $\chi^2 = 32.44$, df = 4, $P < 0.0001$, Table 4.1). The weights of male pupae were also significantly different between plant species (One-way ANOVA: df = 4, F = 28.65, $P < 0.0001$), but female pupal weights did not differ significantly at the 5% level between the host plants (KW: $\chi^2 = 9.38$, df = 4, P = 0.052).

There was no significant correlation observed between the duration of the larval stage and the weight of pupae for female larvae on any of the five studied host plant species. This was also true for males on four different plant species, however, there was a significant (negative) relationship between the duration of the larval stage and the weight of pupae for male larvae only on *Photinia* (Pearson's correlation: t = -3.60, df = 14, P = 0.003; PPMCC: r = -0.69). The mean duration of the larval stage and weight of the pupae for male moths (± SEM) developing on *Photinia* were 38.8 ± 1.92 days and 19.00 ± 0.59 mg, respectively.

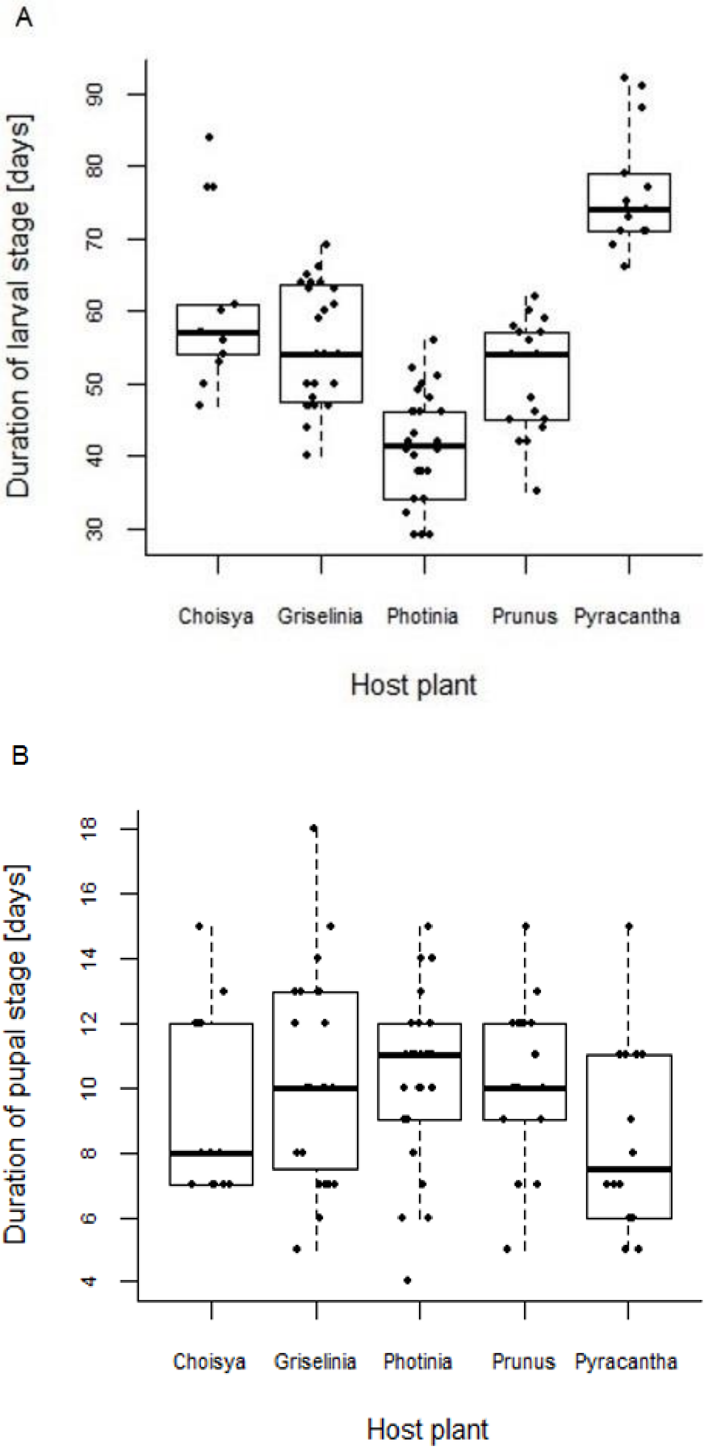


Figure 4.1. Duration of larval (A) and pupal stage (B) for *Cacoecimorpha pronubana* from egg hatch to adult emergence with distinction between five different host plant species; for larvae to grow from hatching to fully formed pupae, and for pupae to undergo pupation up to adult eclosion. Boxes represent the interquartile range (IQR) with a thick horizontal line at the median and whiskers extending to the largest or smallest observation falling within 1.5 IQRs of the upper or lower quantiles. The scattered black dots plotted on each box & whisker represent data distribution along the timeline of the duration of the larval stage on each host plant; the data points were intentionally horizontally spread in order to avoid the points being obscured by each other.

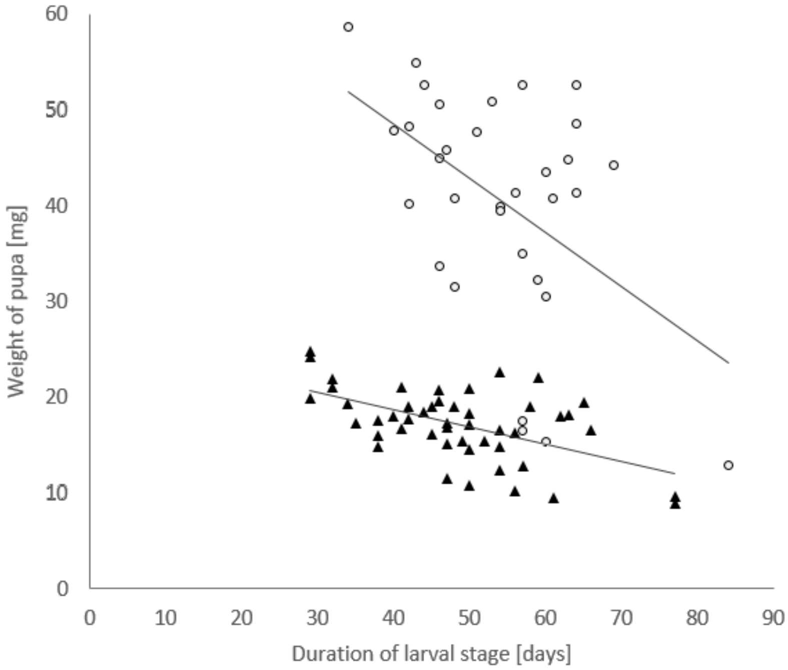


Figure 4.2. Correlation of the duration of larval stage and pupal weights of *Cacoecimorpha pronubana*. There is a moderate negative r = -0.61, y = -0.149x + 24.4, and weak negative correlation r = -0.46, y = -0.475x + 66.7, for male (triangle-shaped data points) and for female (circle-shaped data points), respectively. R-squared indicates that in both instances, either for male ($R^2 = 0.37$; $P < 0.0001$) or female ($R^2 = 0.21$; $P < 0.05$) the duration of larval stage has a weak predictive accuracy on the weight of pupa.

The data, both for duration of the larval stage and the weight of the pupae were then analysed across the whole experiment against sex of the moth. The mean duration of the larval stage and the mean weight of the pupae for male moths (± SEM) was 53.73 ± 2.02 days and 16.40 ± 0.49 mg, and for female moths was 55.91 ± 1.94 days and 40.20 ± 1.99 mg, respectively. The duration of the larval stage was significantly longer for males than for females (Wilcoxon rank sum test with continuity correction: W = 1405.5, P < 0.0001). The weight of female pupae was significantly heavier than those of males (Wilcoxon rank sum test with continuity correction: W = 1405.5, P < 0.0001). The duration of the larval stage and the weight of pupae for males were highly statistically correlated with each other (Pearson's correlation: t = -5.83, df = 57, P < 0.0001) displaying a moderate negative relationship (Pearson's product-moment correlation coefficient (PPMCC: r = -0.61; Figure 4.2). For females the correlation between the duration of the larval stage and the weight of pupae was also statistically significant (Kendall rank correlation: z = -2.21, P = 0.04, τ = -0.26) with a moderate negative relationship (PPMCC: r = -0.48; Figure 4.2).

4.4.4. Fecundity on different host plants

The total numbers of eggs laid by females that had developed on *Choisya*, *Griselinia, Photinia*, *Prunus* and *Pyracantha* were 329, 1212, 2016, 717 and 122, respectively. The mean number of eggs laid per host plant species were 66, 101, 202, 143 and 41, respectively, and they differed significantly among host plants (Pearson's chi-squared test goodness of fit: $\chi^2 = 147.64$, df = 4, $P < 0.001$). There was a significant difference between the number of eggs laid per clutch for moths reared on the five different host plants (KW: $\chi^2 = 64.77$, df = 4, $P < 0.001$). Clutch sizes were significantly different among the six pairs of host plants ($P < 0.05$) (Pairwise comparisons using Wilcoxon rank sum test with P value adjusted by Benjamini and Hochberg (BH) method; Figure 4.3).

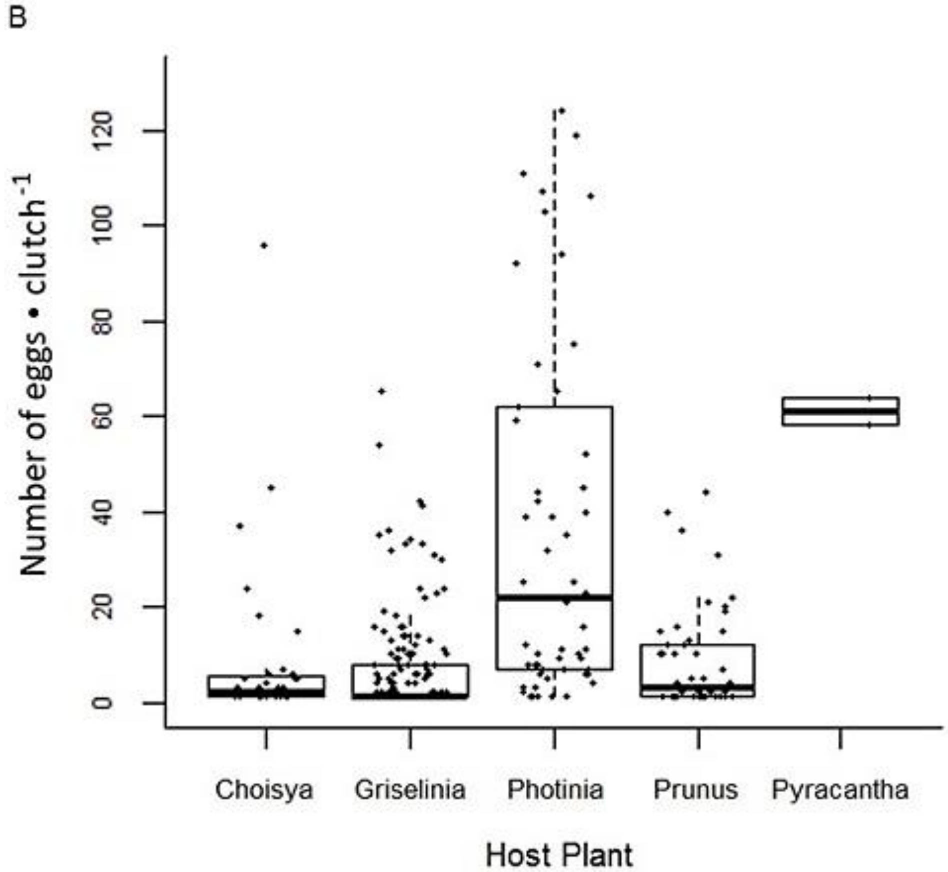
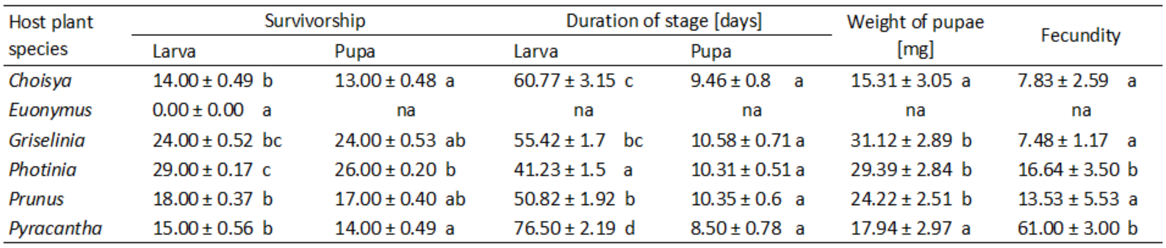


Figure 4.3. Fecundity of the female *Cacoecimorpha pronubana* reared on five different host plants. Fecundity is defined by the eggs•clutch $^{-1}$. Each data point represents a clutch of eggs, where eggs•clutch $^{-1}$ is determined on the y-axis.

Table 4.1. Four life history traits of *Cacoecimorpha pronubana* reared on six different host plants in terms of mean numbers (±SE) of larval and pupal survivorship, duration of larval and pupal stage determined in days, weight of pupa in milligrams, and fecundity defined by the number of eggs in each clutch; na – not applicable (larvae did not survive on *Euonymus*).



Host plant species	Survivorship		Duration of stage [days]		Weight of pupae [mg]	Fecundity
	Larva	Pupa	Larva	Pupa		
Choisya	14.00 ± 0.49 b	13.00 ± 0.48 a	60.77 ± 3.15 c	9.46 ± 0.8 a	15.31 ± 3.05 a	7.83 ± 2.59 a
Euonymus	0.00 ± 0.00 a	na	na	na	na	na
Griselinia	24.00 ± 0.52 bc	24.00 ± 0.53 ab	55.42 ± 1.7 bc	10.58 ± 0.71 a	31.12 ± 2.89 b	7.48 ± 1.17 a
Photinia	29.00 ± 0.17 c	26.00 ± 0.20 b	41.23 ± 1.5 a	10.31 ± 0.51 a	29.39 ± 2.84 b	16.64 ± 3.50 b
Prunus	18.00 ± 0.37 b	17.00 ± 0.40 ab	50.82 ± 1.92 b	10.35 ± 0.6 a	24.22 ± 2.51 b	13.53 ± 5.53 a
Pyracantha	15.00 ± 0.56 b	14.00 ± 0.49 a	76.50 ± 2.19 d	8.50 ± 0.78 a	17.94 ± 2.97 a	61.00 ± 3.00 b

4.5. Discussion

Survival, duration of larval stage, pupal weight and fecundity of *C. pronubana* is significantly affected by larval host plant as has been shown for other species of Lepidoptera (Barbosa *et al.,* 1983; Thiery and Moreau, 2005; Saeed *et al.,* 2010). The faster developing larvae reared on *Photinia* (Rosaceae), *Prunus* (Roseceae), and *Griselinia* (Griseliniaceae) resulted in heavier pupae, while the slower developing larvae on *Pyracantha* (Rosaceae) and *Choisya* (Rutaceae) resulted in lighter pupae. A similar phenomenon was observed for *P. xylostella* by Kahuthia-Gathu *et al.,* (2008). Kahuthia-Gathu *et al.,* (2008) showed that the duration of larval development and pupal weight of the diamondback moth was significantly affected by different Brassicaceae species. As larval performance is dependent on the plant on which it develops, it would appear to be a suitable criterion on which to evaluate host preference (Mayhew, 1998; Gripenberg *et al.,* 2010). It is known that the development and survival of a moth is affected by ovipositional preferences (Leather, 1985; Sarfraz *et al.,* 2011). It is yet to be demonstrated, however, whether survival, development, and fecundity of a moth can predict larval host preference (Bentancourt *et al.,* 2003; Lance, 2012; Kong *et al.,* 2020).

No significant differences in the duration of pupal stages are reported here for *C. pronubana* between host plants. This phenomenon can be also observed among other moth species (Xue *et al.,* 2010; Kirichenko *et al.,* 2011; Razmjou *et al.,* 2014; Reigada *et al.,* 2016).

This study found that the neonatal larvae of *C. pronubana* were unable to survive on *Euonymus japonicus* Thunb. var. *Ovatus Aureus*. It is possible that the first instar larvae were unable to chew through the thick leaf epidermis, and that in the natural environment late-instar larvae migrating from other hosts might infest the host plant (Shelomi *et al.,* 2010; Lance, 2012). Such larvae may perhaps use the more mature foliage as a shelter against predators, where they could develop and emerge as an adult (Bittencourt-Rodrigues and Zucoloto, 2009). Nevertheless, it is not entirely clear, how the abovementioned host affects the larvae differently in natural environments.

A significant correlation between the duration of larval stage and the pupal weight between sexes among the host plant species was only observed on *Photinia* for males. The results from this example showed that the longer duration of larval stage is, or the less suitable food resources are, the greater the negative effect on the development of the adult moth may be. It is possible that *C. pronubana* adult body weight and its reserves are determined by larval food supply (Briegel, 1990). It was further observed that correlations between duration of larval stage and pupal weight in this study differed between sexes. The correlation between the duration of larval stage and the pupal weight for males was moderate, and it was weak among the females. Similar correlations were observed for the fall armyworm moth *Spodoptera frugiperda* (J.E. Smith, 1797) (Pencoe and Martin, 1982). Female pupae were also significantly heavier than those of males as is common in species of Lepidoptera (Lederhouse *et al.,* 1982; Haukioja and Neuvonen, 1985; Leather *et al.,* 1998). It is possible that the correlation between duration of the larval stage and pupal weight occurs because of stress caused by unsuitable food resources. A similar phenomenon was observed for the greater wax moth *Galleria mellonella* (Linnaeus, 1758) (Krams *et al.,* 2015). It has also been shown that nutritional value of a host plant increases the size and the reproductive performance of adult European grapevine moth, *Lobesia botrana* ([Denis and Schiffermüller, 1775]) (Thiery and Moreau, 2005). Such a phenomenon may be a consequence of a higher host plant nitrogen content that accelerates larval development and subsequently weight of adults (Lindroth *et al.,* 1997). It may be possible, that as a result of improving the long-term application of nitrogen fertilizers (or generally synthetic fertilizers), the herbivore feeding preferences, food consumption, and survival, as well as growth, reproduction, and population density of *C. pronubana* may be reduced (Lu *et al.,* 2007). Before applying a control measure to reduce the moth population, it may, however, be economically more viable to estimate, for example, the duration of the larval period for a specific crop prior to selecting the most appropriate control strategy. This may be important where the natural enemy, for example, is effective against only certain larval instars as in the case of the ectoparasitic wasp, *Eulophus pennicornis* Pallas, 1773, which may be used against the tomato moth, *Lacanobia oleracea* (Linnaeus, 1758) (Bell *et al.,* 2005).

Although fecundity, in terms of the total number of eggs laid per host plant, was highest on *Photinia*, and the lowest on *Pyracantha*, the highest number of egg clutches was found on *Griselinia* and *Photinia* and the lowest on *Pyracantha*. Results presented here showed that more fecund adults were observed from the same larval host plants on which the shorter duration of larval development produced heavier pupae. Pupal weight in Lepidoptera is recognised as a good indicator of the fitness of adults and their offspring, and it is known that heavier female adults are more fecund and that they are produced from heavier pupae (Danthanarayana, 1975; Sarfraz *et al.,* 2007). Similar relationships were shown for the diamondback moth, *P. xylostella* females reared on the wild Brassicacea species *R. nudiuscula* Thell. (highest mean fecundity), and on cultivated *Brassica oleracea* L. cultivars (lowest mean fecundity) (Kahuthia-Gathu *et al.,* 2008). Following the Hopkins Host Selection Principle (Hopkins, 1917) it is possible that the oviposition shown in this study is influenced by the larval host plant (Verschut *et al.,* 2017; Gámez and León, 2018).

It is possible that the differences in oviposition behaviour seen in this study, in terms of the size of egg clutches, may also be as a consequence of the foliage density or/and the size of leaves of host plants on which larvae would develop. This phenomenon may be a form of adaptation in terms of a host plant exploitation by the larvae (Davies and Gilbert, 1985). It is possible that the female retains information about the host plant and this affects her oviposition behaviour in developing an oviposition strategy for increased egg survival. Brown and Cameron (1979), for example, showed that there is a strong correlation between decreased size of egg clutches and increased parasitism on the Gypsy moth *Lymantria dispar dispar* (Linnaeus, 1758) eggs. The density factors may play a significant role in the insect’s ovipositional behaviour (Miller and McDougall, 1973; Bigger and Fox, 1997; Myers *et al.,* 1998), but further study on this aspect of the biology of *C. pronubana* is needed.

In natural environments there are many different cues that influence the reproductive choices of an insect (Kagata and Ohgushi, 2002; Mescher and Pearse, 2016; Helms *et al.,* 2017), and subsequently the survival, development and reproductive potential of her offspring (Reavey and Gaston, 1991). The performance of the moth, however, reflects the suitability of a host plant for the larva to feed on, the nutritional value of the available food, and the shelter for the larva to survive (Stockhoff, 1991; Roth *et al.,* 1997; Chen, 2008; Krams *et al.,* 2015). Moth performance is equally likely to be linked to factors such as secondary metabolites, micronutrients, mechanical properties of a host plant or abiotic factors (Du *et al.,* 1998; Dudareva *et al.,* 2004; Colasurdo *et al.,* 2009; War *et al.,* 2012). Assessing and/or determining these factors may be an important aspect in managing integrated pest management systems better. Results from this study support the hypothesis that different host plants have different effects on the performance of individual *C. pronubana*.

Chapter 5. Effect of host plant on the life history of the light brown apple moth *Epiphyas postvittana* (Lepidoptera: Tortricidae)

5.1. Abstract

The light brown apple moth, *Epiphyas postvittana*. (Walker, 1863) (Lepidoptera: Tortricidae) is one of the most polyphagous species of insect known and affects many economically important horticultural crops. Damage to the plants is caused by the larva, which feeds on leaves, flowers or fruits, using silk to tie fruit and leaves together to create a protective shelter. Such behaviour negatively affects the growth and aesthetic appearance of the plants. This study investigated the effects of the host plant on the duration of the larval and pupal stages, the size of these stages and the fecundity of adult female moths. The experiments were completed at 20°C, relative humidity of 60% and a 16L:8D photoperiod. The results indicate that larvae of *E. postvittana* developed 6.2, 6.8 and 16.4 days faster when reared on the cherry laurel, *Prunus laurocerasus* (Rosaceae) than on the New Zealand broadleaf*, Griselinia littoralis* (Griseliniaceae), the Christmas berry, *Photinia* (Rosaceae), and the Mexican orange, *Choisya ternata* (Rutaceae). Compared with the other hosts, the highest number of pupae were collected from *Prunus*. The female pupae were 10.3 mg heavier than the male pupae. There was no correlation between the duration of the larval stage and pupal weight, but host plants significantly affected the duration of larval and pupal stages. Fecundity was determined by the number of eggs laid and the number and size of egg clusters. The highest number of eggs were laid by female moths that developed on *Prunus* as a larva. In all fecundity traits measured, the host plants significantly affected the ovipositional capabilities of the female moth. In this study, it is showed that the host plant has a significant effect on the performance of *E. postvittana,* and that an improved understanding of the life history of this species on its different hosts may be useful in developing improved integrated pest management systems.

5.2. Introduction

The light brown apple moth (Lepidoptera: Tortricidae), (Walker, 1863) is an important polyphagous herbivore pest species affecting a wide range of woody and herbaceous plants, of which many are horticultural crops (Suckling and Brockerhoff, 2010). This species of moth is known to cause damage estimated to be over AUD 21 million per annum in Australia (CABI, 2020). The species affects over 545 plant species in 363 genera from 121 families, and is recognised as one of the most polyphagous insects (Brockerhoff *et al.,* 2011). Although native to Australia (Danthanarayana, 1975; Suckling and Brockerhoff, 2010), the species has extended its range via trade routes with plant material and is now found throughout much of the world. In the UK, it was first reported in the 1930s (CABI, 2020; EPPO, 2020).

Host plants that are important ornamental crop species belong to the families Asteraceae, Cannabaceae, Celastraceae, Fabaceae, (CABI, 2020), Griseliniaceae (personal observation), Grossulariaceae, Lamiaceae, Lauraceae, Oleaceae, Pinaceae, Pittosporaceae, Rosaceae, Rutaceae, Sapindaceae, Solanaceae and Vitaceae (CABI, 2020). Damage to the plant is caused by the highly mobile larva that feeds on the leaves or fruits. It produces silk which it uses to create a shelter rolling leaves together, or to attach leaves to fruits (Lo *et al.,* 2000). Its performance may depend on its ability to overcome physical barriers of the host plant, i.e. trichomes and the thickness of the leaf cuticle and epidermis (Hagen and Chabot, 1986; Zalucki *et al.,* 2002; Shelomi *et al.,* 2010), however, plant chemical compounds, such as volatile compounds, phenolic glycosides, tannins or nutritional value of a host plant (Hemming and Lindroth, 1995) will subsequently determine the larval and adult longevity, body size, fecundity or/and mating and ovipositional behaviour (Brewer, 1985; Lance, 2012; Moreau *et al.,* 2017). Along with environmental conditions, such as temperature (Drake, 1994), rainfall (Rahman *et al.,* 2019), or light intensity (Danthanarayana, 1976), moth performance can be also affected by the trophic interactions within its habitat (Feng *et al.,* 2015; Sayed *et al.,* 2016). Plant volatile compounds being one of the most important determinants of the insect behaviour (Leather, 1995; Coracini *et al.,* 2004; Vuts *et al.,* 2016), are produced by a host plant as a defence response to the herbivore attracting natural enemies of the pest (De Moraes *et al.,* 1998; Paré and Tumlinson, 1999; War *et al.,* 2012).

Epiphyas postvittana is controlled mainly through pesticides and monitoring (CABI, 2020). In response to the negative impacts of synthetic pesticides on the natural environment and human health (Gaines, 1969; Matos *et al.,* 1987; Stenersen, 2004; Damalas and Koutroubas, 2016) growers are, however, increasingly adopting integrated pest management (IPM) practices to control pests (Copping and Menn, 2000; Van Lenteren, 2000). For example, two egg parasitoids, *Trichogramma carverae* Oatman and Pinto and *Trichogramma funiculatum* Carver (Hymenoptera: Trichogrammatidae) are successfully used to control *E. postvittana* in vineyards (Glenn *et al.,* 1997). Sulphur treatments, for example, that are used to control powdery mildew on vines, are, however, harmful to adults and to immature stages of the parasitoid wasps increasing their mortality and reducing fitness. Optimising and integrating the use of biocontrol efficiently, would require changes in the pest management practices, as well as sufficient knowledge on life history parameters of insect species (Thomson *et al.,* 2000). Crop manipulation through diversification practices, such as trap cropping, intercropping, natural enemy refuges, or floral resources for parasitoids and predators, would significantly improve the natural enemies' biodiversity, reduced pest pressure, and increase the yield (Poveda *et al.,* 2008; González-Chang *et al.,* 2019).

Life history attributes and the population structure of the species at any given time within any crop habitat should be carefully considered when developing crop protection systems (Stark *et al.,* 2004). The aim of the study was to improve understanding of the moth performance on ornamental plant species and help in improving crop specific management of the moth more effectively within integrated pest management systems. It was hypothesised that the host plants can affect life history traits of *E. postvittana* differently. This is based on the fact that in another lepidopteran species, the diamondback moth, *Plutella xylostella*, larvae developing on *Brassica oleracea* cultivars produced heavier pupae than larvae developing on wild crucifer species (Kahuthia-Gathu *et al.,* 2008). Pupal weight, however, can reflect duration of larval stage being an important factor for determining host plant suitability for the pest to survive, or ability for the pest to damage a crop (Huang *et al.,* 2018). The objective of the study was to investigate the effect of the host plant on the performance of the light brown apple moth by testing and measuring (i) survivorship of larvae, (ii) duration of larval and pupal stages, (iii) pupal weight, and (iv) fecundity, as well as (v) relationship between duration of the larval stage and the pupal weight.

5.3. Materials and Methods

5.3.1. Host Plants

Six species of ornamental plants were selected for the experiment: the Mexican orange, *Choisya ternata* Kunth 'Lich' (Rutaceae), the Japanese spindle tree*, Euonymus japonicus* Thunb. var. *Ovatus Aureus* (Celastraceae), the New Zealand broadleaf*, Griselinia littoralis* Raoul (Griseliniaceae), the Christmas berry, *Photinia* Lindl. 'Red Robin' (Rosaceae), the cherry laurel, *Prunus laurocerasus* var. *schipkaensis* Späth ex H. L. Späth (Rosaceae), and the firethorn, *Pyracantha angustifolia* (Franch.) C. K. Schneid. (Rosaceae). Plants were propagated from softwood cuttings two years in advance of the beginning of the experiment. The cutting material was collected, propagated and grown in 9-cm diameter black plastic pots in Sinclair® All Purpose Growing Medium Compost (Sinclair Pro, UK) under protected glasshouse conditions at an ornamental plant nursery in Shropshire, UK (52°37'20'' N, 2°15'20'' W; 119 m a.s.l). The choice of the plant species for the experiment was based on their high susceptibility to *E. postvittana* at abovementioned plant nursey.

5.3.2. Insects

Cultures of *E. postvittana* were established using adult moths caught between April and June 2018 at the same ornamental plant nursery in Shropshire, UK, from which the plants were obtained. The moth culture was established in a BugDorm-4D® Insect Rearing Cage (47.5 x 47.5 x 47.5 cm) (MegaView, Taiwan) placed in a Fitotron® SGR plant growth room (Weiss Technik, UK) under controlled environmental conditions: temperature, relative humidity and photoperiod, of 20°C, 60% and 16 hours, respectively. Moths were reared on a mix of ornamental plants belonging to the Caprifoliaceae, Hypericaceae, Pittosporaceae, Plantaginaceae and Rhamnaceae families. The moth colony was maintained from June 2018 to November 2018. No additional individuals were introduced after the initial establishment and during the maintenance of the culture. Neonate larvae used for the experiment were collected from the second generation when they were 0–34h old.

5.3.3. Experiments

In October 2018 plants were moved from the glasshouse into the laboratory in a Fitotron® SGR plant growth room (Weiss Technik, UK) under the same controlled environmental conditions as used to maintain the culture of *E. postvittana*. In October 2018, at the time of the experiment, plants were well established, matured, continuing their slow vegetative growth. Their height varied from 20 to 25 cm, and their mid-width measured approximately 12 cm. The experiment was set up in a Fitotron® SGR 'Walk-in' plant growth room under the same controlled environmental conditions as used to maintain the culture of *E. postvittana*. The treatments consisted of the six host plants – *Choisya*, *Euonymus, Griselinia*, *Photinia*, *Prunus* and *Pyracantha*. Each replicate consisted of a single plant of each and six replicates were laid out using a Latin Square design (Fisher, 1925). Five *E. postvittana* larvae were placed on each host plant. The larvae were collected from the culture and placed on each plant using a fine paintbrush. Each time, after total of five larvae were placed on a leaf, plant was immediately covered with a nylon mesh sleeve (43 cm long by 13 cm diameter; mesh aperture area = 16 qm^2, A^o = 50%). The sleeves were closed at the top and the bottom in order to isolate plants from each other. Plants were stood on a black plastic tray and were watered as required from beneath. In total, there were 36 plants and 180 larvae used for the experiment. Pupae were transferred separately into Petri dishes (90 mm diameter x 15 mm height), and placed in the same room under the same environmental conditions. Each Petri dish had a circular piece of dry plain white paper towel placed on the bottom of the dish. The following data were recorded: larval stage duration; date of pupal formation and the weight of the pupa; as well as date of adult emergence and its weight. After emergence, the female moths were allowed to mate with an introduced male and lay eggs; males came from the same host plant species as the females. Up to three females were paired with the same number of males and placed in one Petri dish, where subsequently the eggs were laid. The total number of eggs laid by females reared on each host plant was recorded.

5.3.4. Statistical Analysis

Analyses were completed using R version 4.0.2. (R Core Team, 2020), and the significance level was set at α=0.05. The analyses focused on the effect of the host plants on the chosen life history attributes of the moth; duration of larval and pupal stage, pupal weight, and fecundity. They were performed only on moths that completed their life cycle – from egg hatching to oviposition. Analyses did not include *Euonymus and Pyracantha* as larvae did not survived on these two host plants. Therefore, larval survivorship was compared between six, and pupal survivorship between four host plant species, so it was duration of larval and pupal stage, and correlation between duration of larval stage and pupal weight. Fecundity, however, was measured on three host plant species as low number of adults that emerged include low number of females that were unable to produce eggs.

5.3.4.1. Larval and pupal survivorship

The number of larvae and pupae that survived was determined by the number of pupae and adults collected. Larval survivorship was determined by the total number of pupae collected, and the pupal survivorship was determined by the total number of adults collected.

Larval survivorship was compared between six host plant species, and pupal survivorship between four host plant species (analyses did not include *Euonymus* and *Pyracantha*). Both attributes were statistically analysed using Kruskal-Wallis rank sum test (One-way ANOVA on ranks). The null hypothesis was that the medians of all groups are equal with no significant difference in survival rates between the host plant species.

For multiple pairwise-comparisons Wilcoxon rank sum test was used with P value adjusted by Benjamini and Hochberg (BH) method. To check the differences within the median numbers between larvae applied and larvae survived, as well as between pupae collected and pupae survived, Wilcoxon signed rank test was used with continuity correction. The null hypothesis for both attributes was that there are no significant differences in median numbers before and after collection.

5.3.4.2. Duration of larval and pupal stage

The duration of the larval stage was measured from hatching to pupation, and the duration of the pupal stage was measured from pupation to eclosion. The duration of each stage of development was recorded in days, and analysed for both larvae and pupae originating from four different species of host plants. The Shapiro-Wilk test was used to test the assumption of Gaussian distribution of residuals, whereas homogeneity of variance was tested with Levene’s test. Kruskal-Wallis rank sum test was used to evaluate differences between the mean duration of the larval stage and the duration of the pupal stage. Wilcoxon rank sum test with P value adjusted by Benjamini and Hochberg (BH) method was used for pairwise comparisons between the groups of host plants.

5.3.4.3. Correlation between duration of larval stage and pupal weight between sexes

The distribution of data for the duration of larval stage and pupal weight between sexes was tested across the whole experiment with the Shapiro-Wilk test. The homogeneity of variances for the duration of larval stage a non-parametric Fligner-Killeen test was used, and the Levene’s test for pupal weight. In order to compare the median duration of larval stage and the median weight of pupa between males and females, non-parametric unpaired two-sample Wilcoxon test was used.

The significance of correlation, its strength and the direction were tested with Pearson product-moment correlation coefficient (PPMCC). When the data were not normally distributed the Kendall rank correlation coefficient (tau) test was used to estimate a rank-based measure of association. When the correlation was significant ($P < 0.05$), the R-squared was used to indicate the strength of predictive accuracy.

5.3.4.4. Correlation between duration of larval stage and pupal weight, between sexes on different host plants

The distribution of data for the duration of larval stage and pupal weight between sexes, and between sexes on different host plants was tested with the Shapiro-Wilk test. The significance of correlation, its strength and the direction were tested with Pearson product-moment correlation coefficient (PPMCC). When the data were not normally distributed the non-parametric Spearman rank correlation coefficient (rho) test was used to estimate a rank-based measure of association. When the correlation was significant ($P < 0.05$), the R-squared was used to indicate the strength of predictive accuracy.

5.3.4.5. Fecundity on different host plants

Fecundity of each moth was determined by the number of eggs laid following development on each host plant. The Shapiro-Wilk test was used to test the assumption of Gaussian distribution of residuals, and the homogeneity of variances was analysed with Levene's Test. The differences between the means of fecundity on three different host plants were analysed with Pearson’s chi-square test.

To test the differences between the numbers of eggs laid per cluster on three different host plants, Kruskal-Wallis rank sum test was used. The Wilcoxon rank sum test was used for pairwise comparisons to test the differences between the numbers of eggs laid per cluster between the host plants. The P value of the test was adjusted by Benjamini and Hochberg (BH) method.

5.4. Results

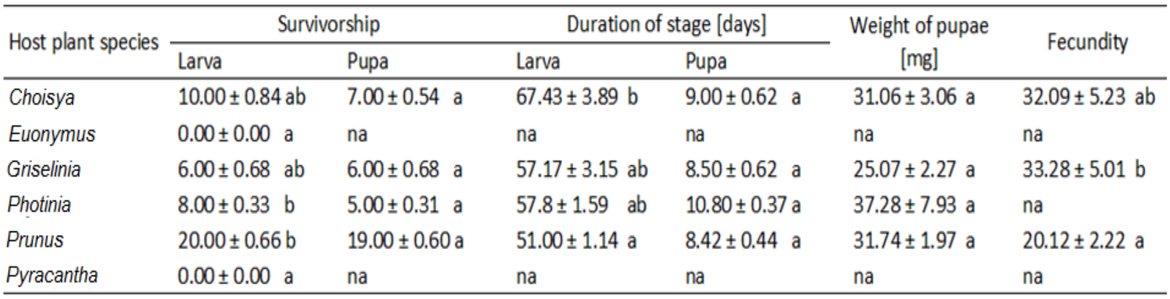
5.4.1. Larval survivorship

Larval survivorship was determined by the number of pupae collected from five different host plant species - *Choisya*, *Euonymus, Griselinia, Photinia*, *Prunus* and *Pyracantha.* Survival rates differed significantly between six host plant species for larvae (Kruskal-Wallis chi-squared = 18.91, df = 5, P = 0.002), and did not differ between four host plant species for pupae (KW = 7.7614, df = 3, P = 0.051).

Multiple pairwise-comparisons Wilcoxon rank sum test (MPCW) for larvae indicated significant differences in survivorship between four pairs of host plants (P < 0.05): *Euonymus and Photina*, *Euonymus* and *Prunus*, *Pyracantha* and *Photinia*, and *Pyracantha* and *Prunus.* The remaining eleven pairs did not differ significantly. The same test did not indicate differences for pupal survivorship between four tested host plants (Table 5.1).

The difference between the total number of larvae applied initially, and larvae survived (pupae collected) on six host plants was statistically significant (Wilcoxon rank sum test with continuity correction: W = 1296, P < 0.0001). The difference between pupae collected, and pupae survived among four host plants (pupal mortality) was statistically significant (Wilcoxon rank sum test with continuity correction: W = 151.5, P = 0.002).

Table 5.1. Life history traits of *Epiphyas postvittana* reared on six different host plants in terms of mean numbers (±SE) of larval and pupal survivorship, duration of larval and pupal stage (days), weight of pupa (mg), and fecundity defined by the number of eggs in each clutch; na – not applicable (larvae did not survive on *Euonymus* and *Pyracantha*). Values in each column with the same letter are not significantly different (P > 0.05), Wilcoxon rank sum test with P-values adjusted by Benjamini and Hochberg (BH) method.



Host plant species	Survivorship		Duration of stage [days]		Weight of pupae [mg]	Fecundity
	Larva	Pupa	Larva	Pupa		
Choisya	10.00 ± 0.84 ab	7.00 ± 0.54 a	67.43 ± 3.89 b	9.00 ± 0.62 a	31.06 ± 3.06 a	32.09 ± 5.23 ab
Euonymus	0.00 ± 0.00 a	na	na	na	na	na
Griselinia	6.00 ± 0.68 ab	6.00 ± 0.68 a	57.17 ± 3.15 ab	8.50 ± 0.62 a	25.07 ± 2.27 a	33.28 ± 5.01 b
Photinia	8.00 ± 0.33 b	5.00 ± 0.31 a	57.8 ± 1.59 ab	10.80 ± 0.37 a	37.28 ± 7.93 a	na
Prunus	20.00 ± 0.66 b	19.00 ± 0.60 a	51.00 ± 1.14 a	8.42 ± 0.44 a	31.74 ± 1.97 a	20.12 ± 2.22 a
Pyracantha	0.00 ± 0.00 a	na	na	na	na	na

5.4.2. Duration of larval and pupal stage

The mean duration of the larval and pupal stage across the whole experiment was 56 ± 1.46 days and 9 ± 0.30 days, respectively. Host plant had a significant effect on the duration of the larva (Kruskal-Wallis rank sum test (KW): chi-squared = 17.30, df = 3, $P < 0.001$) and on the duration of pupal stage between the host plants (KW: chi-squared = 7.88, df = 3, $P < 0.05$; Figure 5.1B). There was a significant difference in duration of the larval stage only between *Choisya and Prunus* (P = 0.002) (Multiple pairwise-comparison between groups using Wilcoxon rank sum test, P value adjustment method: BH; Figure 5.1A). Despite the overall effect of host plant treatment on pupal duration, *post hoc* analysis did not indicate significant differences between any of the pairs (Table 5.1).

5.4.3. Correlation between duration of larval stage and pupal weight

The mean duration of the larval stage and the mean weight of the pupae for male moths (± SEM) was 55.81 ± 1.95 days and 26.81 ± 1.23 mg, and for female moths was 56.31 ± 2.27 days and 37.14 ± 2.83 mg, respectively. The were no differences between the host plants for mean weight of pupa (KW = 3.7755, df = 3, P = 0.286) (Table 5.1).

As the female pupae were significantly heavier than those of males (Wilcoxon rank sum test with continuity correction: W = 257.5, P = 0.006), the data for duration of the larval stage and the weight of the pupae were analysed across the whole experiment against sexes.

For males, the duration of the larval stage and the weight of pupae were not statistically correlated with each other (Spearman Rank Correlation coefficient (SRCC): S = 1560.1, $P > 0.05$; Spearman's correlation coefficient (rho): $\rho = -0.013$; Figure 5.2A). The correlation between the duration of the larval stage and the weight of pupae for females was not statistically significant (SRCC: S = 754.2, $P > 0.05$; SCC: $\rho = -0.110$; Figure 5.2B).

5.4.4. Correlation between duration of larval stage and pupal weight, between sexes on different host plants

There were no significant relationships observed between the duration of the larval stage and the weight of pupae between sexes on different host plants.

Correlation between the duration of the larval stage and the weight of pupae for males on *Choisya* (Pearson's correlation (PC): t = -0.004, df = 1, P = 0.997; PPMCC: r = -0.004), *Griselinia* (PC: t = 0.52, df = 1, P = 0.693; PPMCC: r = 0.46), *Photinia* (PC: t = -0.76, df = 1, P = 0.587; PPMCC: r = -0.60) and *Prunus* (PC: t = -0.05, df = 10, P = 0.959; PPMCC: r = -0.02) were not statistically correlated.

The correlation for females on *Choisya* (PC: t = -0.10, df = 2, P = 0.423; PPMCC: r = -0.58), *Griselinia* (PC: t = -0.18, df = 1, P = 0.887; PPMCC: r = -0.18), *Photinia* (PC: t = 0.52, df = 1, P = 0.997; PPMCC: r = 0.46) and *Prunus* (PC: t = 1.33, df = 5, P = 0.242; PPMCC: r = 0.51) were also not significant.

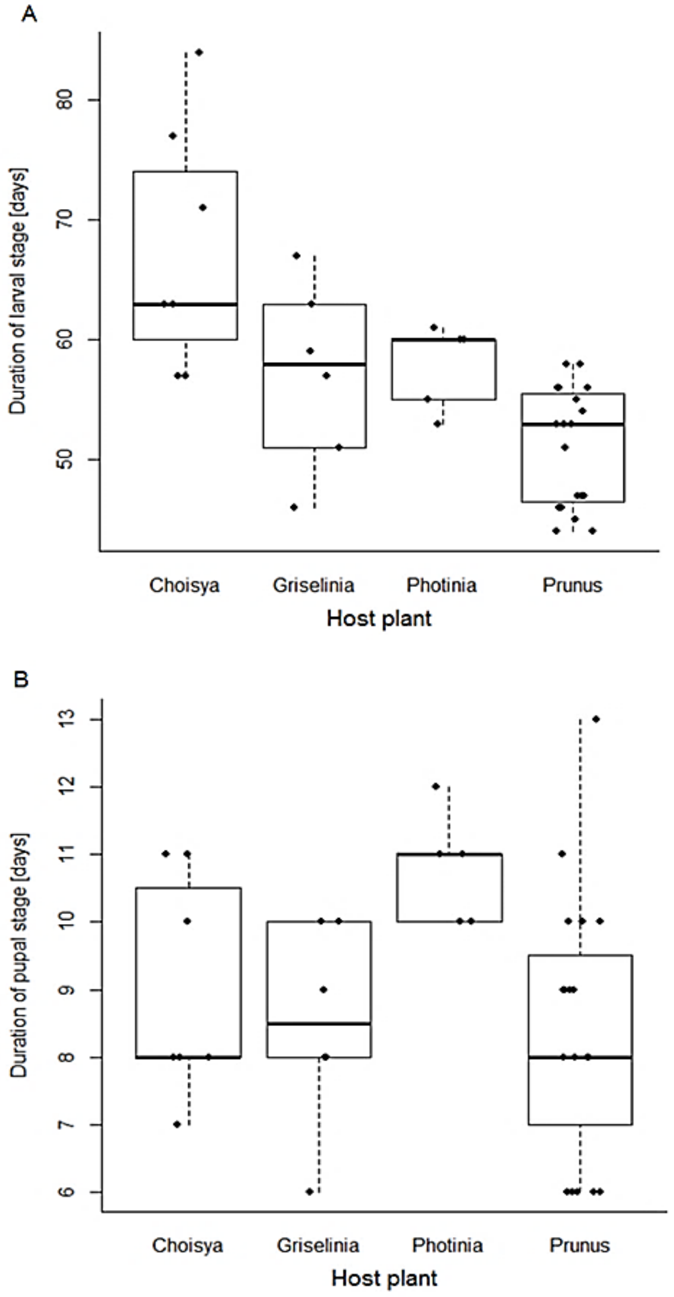


Figure 5.1. Duration of larval and pupal stage for *Epiphyas postvittana* are presented here from egg hatch to adult emergence with distinction between four different host plant species. Boxes represent the interquartile range (IQR) with a thick horizontal line at the median and whiskers extending to the extrema of the observations falling within 1.5 IQRs of the upper or lower quantiles. The scattered black dots plotted on each box and whisker represent data distribution. The data points were intentionally horizontally spread in order to avoid the points being obscured by each other.

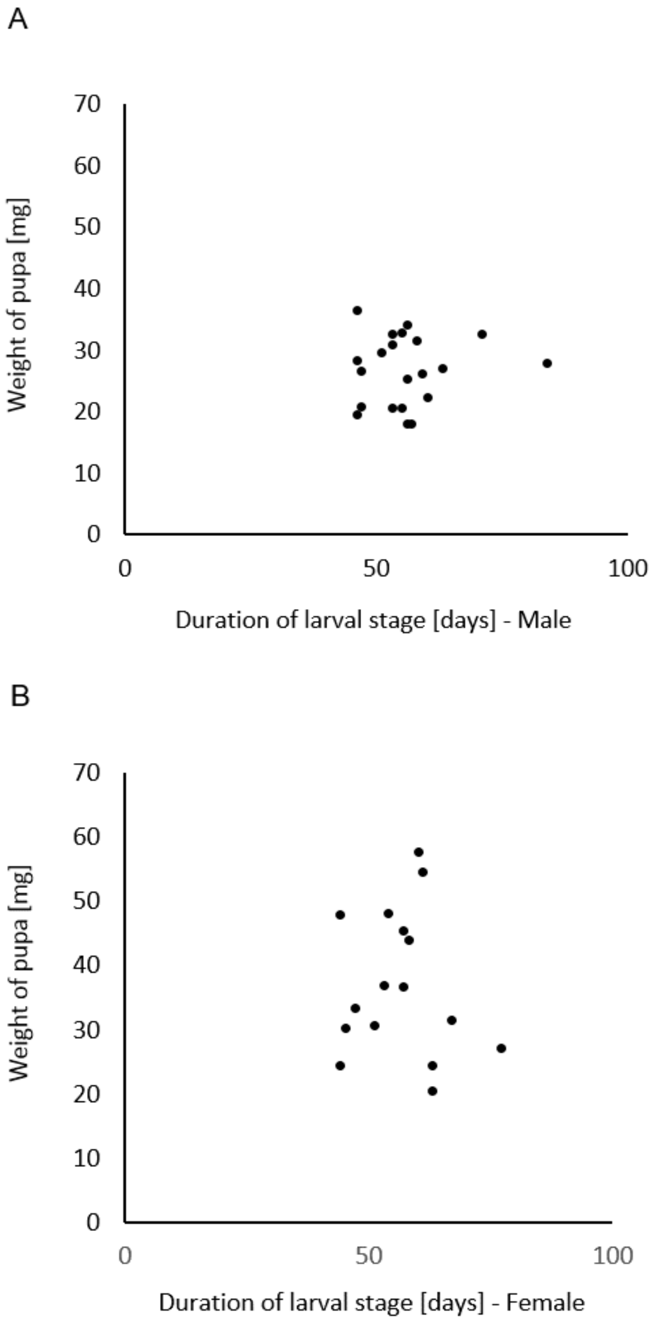


Figure 5.2. Correlation of the duration of larval stage and pupal weights of *Epiphyas postvittana*. There is a weak positive r = 0.09, y = 0.0566x + 23.651, and weak negative correlation r = -0.10, y = -0.1192x + 43.848, for male – A, and female – B, respectively. In both instances, correlations between the duration of larval stage and the pupal weight is statistically not significant. Either for male ($R^2 = 0.008$; $P > 0.05$) or female ($R^2 = 0.0091$; $P > 0.05$) the duration of larval stage has no predictive accuracy on the weight of pupa.

5.4.5. Fecundity on different host plants

Female moths that developed on *Photinia* did not produce any eggs. The mean number of eggs laid by each female moth were 177, 277, 382 for *Choisya, Griselinia* and *Prunus*, respectively; the numbers differed significantly between host plant species (Pearson's chi-square test: chi-squared = 75.419, df = 2, $P < 0.001$; Chi-squared test for given probabilities; Figure 5.3A). There was a significant difference between the number of eggs laid per clutch for moths reared on the three different host plants (Kruskal-Wallis rank sum test: chi-squared = 16.07, df = 2, $P < 0.001$). There were significant differences in the number of eggs laid per clutch between two groups of host plants: *Choisya* and *Prunus*, and *Griselina* and *Prunus* ($P < 0.05$); there was no significant deference between *Choisya* and *Griselinia* ($P > 0.05$) (Pairwise comparisons using Wilcoxon rank sum test with P value adjusted by Benjamini and Hochberg (BH) method; Table 5.1., Figure 5.3B).

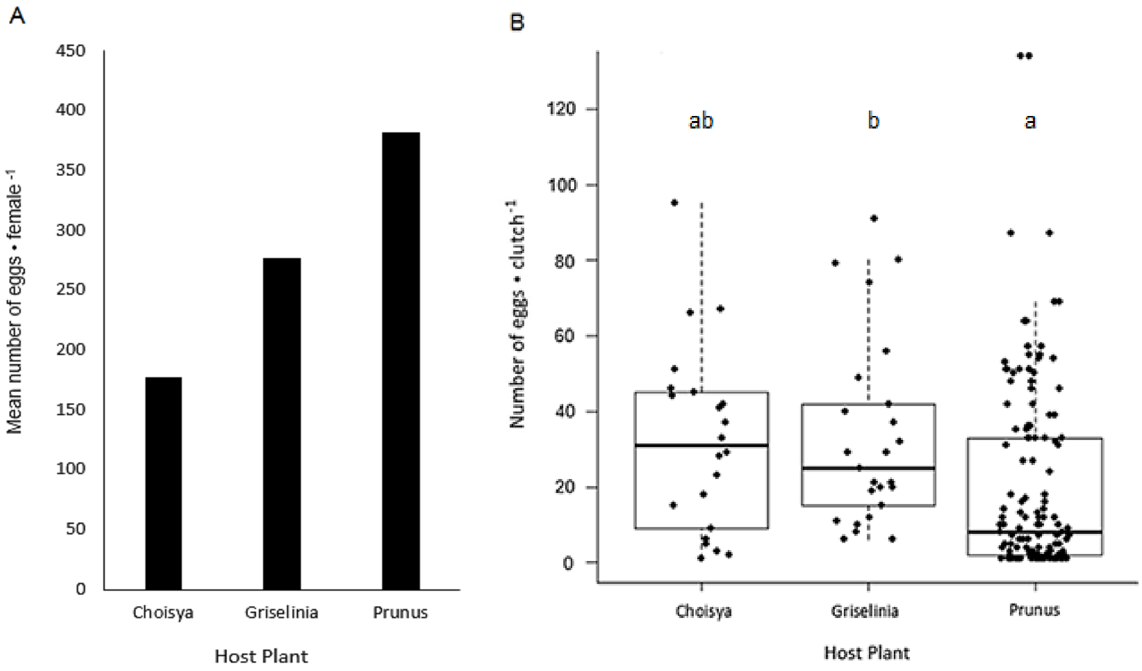


Figure 5.3. Fecundity of the female *Epiphyas postvittana* on three different host plants. A – fecundity per host plant is defined by the mean number of eggs•female $^{-1}$ (mean ± SE). B – fecundity is defined by the eggs•clutch $^{-1}$. Each data point represents a clutch of eggs, where eggs•clutch $^{-1}$ is determined on the y-axis. The same letters (present above each box & whisker) between each host plant species indicate that data are not significantly different ($P > 0.05$), Wilcoxon rank sum test with P-values adjusted by Benjamini and Hochberg (BH) method. The scattered black dots plotted on each box and whisker represent distribution of the data reflected by the effect of a host plant on the development of the larva; the data points were intentionally horizontally spread in order to avoid the points being obscured by each other.

5.5 Discussion

The results from this study showed that the survival rates, larval and pupal duration, and fecundity of *E. postvittana* is affected by the host plant on which it is reared. This is similar to previous studies with other species of Lepidoptera (Barbosa *et al.,* 1983; Thiery and Moreau, 2005; Saeed *et al.,* 2010). No correlations, however, were observed between duration of the larval stage and the weight of pupa.

Although duration of the larval stage for *Griselina* and *Photinia* was the same, larvae developed fastest on *Prunus*, and the slowest on *Choisya* (Rutaceae). Larvae that developed on *Photinia* (Rosaceae) resulted in the heaviest pupae and adults, but the larvae that developed on *Griselinia* (Griseliniaceae) produced the lightest pupae and adults. Similar correlations were found for the diamondback moth *Plutella xylostella*, on cultivated *Brassica oleracea* cultivars and wild crucifer species (Kahuthia-Gathu *et al.,* 2007). Additionally, it was noted that host plants in this study also affected the duration of pupal stages, which is not a common phenomenon in other moth species (Pencoe and Martin, 1982; Xue *et al.,* 2010; Sun *et al.,* 2015; Reigada *et al.,* 2016).

The results from this study showed that the neonatal larvae of *E. postvittana* were unable to survive on *Euonymus japonicus* Thunb. var. *Ovatus Aureus* (Celastraceae), and on the firethorn *Pyracantha angustifolia* (Rosaceae). It was noted, that the neonatal larvae were apparently unable to chew through the cuticle or/and a leaf epidermis, and it is possible that in natural environments these host plants are affected only by the late-instar larvae moving from surrounding vegetation (Lance, 2012). As it was observed in the experiment carried in this study, it is not apparent, whether the size or morphological features of the leaves affected the survival and the development of the larva, chemical composition of the host plant, or physio-chemical characteristics of the matured host. As both the chemical composition of the host plant changes throughout the growing season (Hull *et al.,* 1975; Fernandez-Escobar *et al.,* 1999; Haukioja *et al.,* 2002; Ojeda-Avila *et al.,* 2003), and leaves become tougher as they mature (Lawson *et al.,* 1984; Fernandez-Escobar *et al.,* 1999; Haukioja *et al.,* 2002), they can significantly affect the survival and the duration of larval and pupal stages (Hough and Pimentel, 1978; Lawson *et al.,* 1984).

Not only leaf morphology or plant derived chemical compounds determines the ability of the larva to survive (Fordyce and Agrawal, 2001; Horgan *et al.,* 2007; Žnidarčič *et al.,* 2008) but also nutritional value of the plant components (Ojeda-Avila *et al.,* 2003; Marazzi and Städler, 2004). As such, better adapted larvae use mature leaves more efficiently and have a higher growth rates, whereas less adapted species compensate their slower growth rate with an increased duration of the larval period (Schroeder, 1986). For example, the gypsy moth, *Lymantria dispar* (Linnaeus, 1758) (Lepidoptera: Erebidae) can accelerate larval development and increase weight of adults if host plant nitrogen content increases (Lindroth *et al.,* 1997). Similarly, an increase in the weight of pupae in the forest tent caterpillar moth *Malacosoma disstria* Hübner, 1820 (Lepidoptera: Lasiocampidae) has also been recorded as nitrogen content of the host plant increases (Hemming and Lindroth, 1995).

Correlation between the duration of the larval stage and pupal weight in this study was analysed between host plants species and sexes of the larva as a result of the significant differences in pupal weights between male and female larva. From the results of this study it was found that the female pupae were significantly heavier than those of males, which aligns with other studies on moth species (Lederhouse *et al.,* 1982; Haukioja and Neuvonen, 1985; Leather *et al.,* 1998). These results showed, however, that there is no correlation between those two attributes, neither for male, nor for female larva. It was concluded that the polyphagous nature of *E. postvittana* may reflect its better adaptation to unsuitable food resources displaying a stronger spatial dispersal behaviour, than those of other species of Lepidoptera (York and Oberhauser, 2002; Krams *et al.,* 2015). Spatial distribution and behavioural plasticity of the insect may occur in order to increase egg survival, or disperse eggs across a large area as the form of initial recognition and adaptation of the moth to new habitats (Awmack and Leather, 2002; Suckling and Brockerhoff, 2010; Carrasco *et al.,* 2015). Perhaps this may be a tactic that evolved in response to natural enemies of the pest. For example, differences in the spatial distribution and parasitism levels of egg parasitoids, *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) may widely vary within habitats or specific host species depending on the plant on which the eggs are found (Romeis *et al.,* 2005).

Fecundity, in terms of the total number of eggs laid per larval host plant, was highest on *Prunus*, and the lowest on *Choisya*. The highest number of egg clutches in this study was found also on *Prunus* and the lowest on *Griselinia* and *Choisya*. As it was observed, females that were more fecund, developed as a result of the shortest duration of larval stage, and the highest survival rate. Although, pupal weight is often a good indicator of the fitness of adults (Danthanarayana, 1975; Sarfraz *et al.,* 2007), this relationship was not observed in this study. As the oviposition of *E. postvittana* female moths significantly differed between larval host plants, recorded fecundity may reflect the feeding behaviour of the larva that was affected by the host plant on which it developed. This would imply that the female adult moth oviposition behaviour is predetermined by larval experience (Miller and McDougall, 1973; Davies and Gilbert, 1985; Bigger and Fox, 1997; Myers *et al.,* 1998). Following the Hopkins Host Selection Principle (Hopkins, 1917) it is possible that females may make trade-offs that are influenced by the larval host plants. For example, larger clutches laid on a host plant that is different to the host on which the moth developed may be an advantage in terms of an egg survival, but the same behaviour can be driven by responses to parasitism, with large clutch sizes tending to suffer from lower rates of parasitism (Beckage and Riddiford, 1983; Geervliet *et al.,* 1998; Stuart and Polavarapu, 2000; Randlkofer *et al.,* 2007). Size of the clutch may be additionally regulated by food availability (Godfray *et al.,* 1991), and the ability of neonate larvae to build an effective shelter, which may influence survival rates (Damman, 1987).

Survival, development, performance and reproductive choices of an insect may be affected by many different cues in the natural environment (Kagata and Ohgushi, 2002; Mescher and Pearse, 2016; Helms *et al.,* 2017). Specific characteristics of a host plant, however, can determine the life history of the moth in many ways. Suitability of a host plant for the larva to feed on, however, may inevitably reflect the performance of the moth, as well as, its behavioural traits (Stockhoff, 1991; Colasurdo *et al.,* 2009; Carrasco *et al.,* 2015). Pest management practices in such crop environments may require a diversification and manipulation of the crop protection and cultural methods used to grow ornamental crops, in order to increase crop biodiversity, reduce pest pressure, and intoxication of the local environment. Determining nutritional values of the host plants may be an important aspect for improving the manipulations of crop habitats and introducing more efficient integrated pest management systems. In this study, it was shown that the host plants had a significant effect on the developing larvae. Therefore, the results support the hypothesis, that host plants affect the performance of *E. postvittana*.

Chapter 6. A comparison of the relative performance of two species of moth, *Cacoecimorpha pronubana* and *Epiphyas postvittana*, on different host plant species.

6.1. Abstract

The carnation tortrix moth, *Cacoecimorpha pronubana* (Roelofs and Brown, 1982), and the light brown apple moth, *Epiphyas postvittana* (Walker, 1863) (Lepidoptera: Tortricidae) are two important polyphagous pest species affecting a wide range of plant species of which many are horticultural crops. Damage to the crop is caused by the larvae of these two moths rolling leaves together and feeding of the foliage. In order to understand how these two species are affected by a host plant through transgenerational dietary changes, it was hypothesised that life history traits of the larvae developing on one host plant species can be affected differently in further generations by different host plants, and that both species may exhibit similar patterns in their life history due to sudden dietary changes. The performance of several life history traits of *C. pronubana* and *E. postvittana* was compared on three host plant species – *Prunus* (Rosaceae), *Choisya* (Rutaceae) and *Griselinia* (Griseliniaceae). For the experiment second generation larvae ware used of *C. pronubana* and *E. postvittana* reared exclusively on *Prunus*, and second-generation larvae reared exclusively on *Griselinia*. Significant differences in performance were observed between these two moths and between their cultures from which they originated. Apart from survivorship, *C. pronubana* larvae developed more slowly (70.65 ± 2.02 days) than *E. postvittana* (46.01 ± 1.20 days), resulting in 8.28 mg smaller pupae (23.31 ± 1.02 mg). Even though greater size clutches were produced by *E. postvittana* (21.31 ± 1.98 eggs per clutch), *C. pronubana* was significantly more fecund in terms of the mean number of eggs laid per female. Both moths, and their cultures exhibited similar patterns across clutch sizes, indicating that sudden change in diet experienced by a larva have a significant effect on the oviposition behaviour of the adult female. As a result, this may affect their population dynamics and the degree at which crop habitat may be affected. Such phenomenon may be an important mechanism that regulate local migrations of these two herbivore species, and it may need to be considered in developing new strategies for improving the integrated pest management systems in crop environments.

6.2. Introduction

The carnation tortrix moth (Lepidoptera: Tortricidae) (Roelofs and Brown, 1982) and the light brown apple moth (Lepidoptera: Tortricidae), (Walker, 1863) are economically important polyphagous pest species affecting together over 500 plant genera (Kacar and Ulusoy, 2008; Brockerhoff *et al.,* 2011; Pencheva and Yovkova, 2016; Reddy, 2016). Both moth species affect a wide range of woody and herbaceous plants, of which many are important horticultural crops (Fisher, 1924; Brown *et al.,* 2010; Suckling and Brockerhoff, 2010). The moths have been present in Britain since at least 1905 and 1930, respectively (Fisher, 1924; CABI, 2020; EPPO, 2020).

Damage to the plant is caused by the larva that feeds on the foliage or fruits. It produces silk and uses it to roll leaves together to protect itself against predators and natural enemies (Fisher, 1924; Bestagno, 1955; Lo *et al.,* 2000). Host plants, that are known to be a common dietary source for both moth species belong to the families Asteraceae, Fabaceae (CABI, 2020), Griseliniaceae (personal observation), Oleaceae, Rosaceae, Rutaceae, Solanaceae (Beitia *et al.,* 2016; CABI, 2020).

Most synthetic pesticides that are used to control these pests are harmful to the environment and human health (Gaines, 1969; Matos *et al.,* 1987; Solomon *et al.,* 2001; Stenersen, 2004; Rehman *et al.,* 2014; Wang *et al.,* 2014; Damalas and Koutroubas, 2016). In nature, species of Lepidoptera are controlled by their enemies, e.g., *C. pronubana* on olive trees is controlled by at least eight species of parasitoids and predators (Kacar and Ulusoy, 2012), and *E. postvittana* by over 25 parasitoid wasps known (Feng *et al.,* 2015), of which *Dolichogenidea tasmanica* (Cameron, 1912) (Hymenoptera: Braconidae) is one of the widest recognised parasitoid of larvae of this moth (Feng *et al.,* 2015; Yazdani, 2015). It was shown, however, that insecticides (e.g., neonicotinoids and pyrethroids) are harmful to non-target insects, such as *Trichogramma evanescens* Westwood, 1833 (Hymenoptera: Trichogramma) a parasitic wasp of *C. pronubana* eggs (Wang *et al.,* 2014). Yet, there are approximately 17,000 species of braconids recognised worldwide, and over 25,000 species are still to be described (Jones, 2009), and yet, toxicity of pesticides to most of these species is unknown.

In order to reduce the deleterious effect of pesticides in the crop habitat, many growers consider the adoption of integrated pest management (IPM) practices to control pests (Copping and Menn, 2000; Van Lenteren, 2000). IPM is an effective approach to pest management that relies on a combination of comprehensive information on the life cycles of pests and their interaction with a crop habitat (Dhawan and Peshin, 2009). Performance of a moth may be affected by various abiotic factors and biotic factors such as the host plant, which is known to be one of the most important determinants of developing larvae, further affecting pupal size, adult fitness and longevity, as well as fecundity and ovipositional behaviour (Brewer, 1985; Lance, 2012; Moreau *et al.,* 2017). It is unclear, however, how the performance of either species of moth may be affected by generational dietary changes, and how these changes may further affect larval performance, adult behaviour, and overall performance. This knowledge may be useful in developing more efficient practices within the IPM systems. Predicting the changes in the life history attributes of the moth species may improve the efficiency of the parasitism of controlled pests.

It was hypothesised that there is a significant difference between the life history traits of these two moth species in regard to the crop they may affect. The effect of host plants, along with generational or seasonal dietary changes may affect the life history parameters of *C. pronubana* and *E. postvittana*. This in turn may change the population dynamics or spatial distribution behaviour of both species.

6.3. Materials and methods

6.3.1. Host plants

Plant material was grown and obtained from an ornamental plant nursery in Shropshire, UK (52°37’20’’ N, 2°15’20’’ W; 119 m a.s.l.). Plants were propagated from softwood cuttings two years before the beginning of the experiment. The cutting material was collected, propagated and grown in 9-cm diameter black plastic pots filled with Sinclair® All Purpose Growing Medium Compost (Sinclair Pro, UK) under protected glasshouse conditions. For the maintenance of the moth cultures designated for the use in setting up the experiment, and for the experiment itself, following host plants species were used: *Prunus laurocerasus* var. *schipkaensis* Späth ex H. L. Späth (Rosaceae), *Choisya ternata* Kunth ‘Lich’ (Rutaceae), and *Griselinia littoralis* Raoul (Griseliniaceae).

6.3.2. Insects

Two moth species – *Cacoecimorpha pronubana* and *Epiphyas postvittana* were collected in May 2018, from the same ornamental plant nursery form which the host plants were obtained. Initially two moth cultures were established in two separate BugDorm-4D® Insect Rearing Cages (47.5 x 47.5 x 47.5 cm) (MegaView, Taiwan) placed in a Fitotron® SGR plant growth room (Weiss Technik, UK) maintained at a constant temperature 20°C, 60% RH and 16L:8D photoperiod. Moths were reared on a mix of Caprifoliaceae, Hypericaceae, Pittosporaceae, Plantaginaceae and Rhamnaceae. In September 2018 four new moth cultures were initiated using second generation larvae collected from the existing two cultures, one for each moth species reared exclusively on *Prunus* (Rosaceae) and one for each species reared exclusively on *Griselinia* (Griseliniaceae). As a result, four moth cultures (pre-treatments) were established: *C. pronubana* reared on *Prunus* and on *Griselinia*, and *E. postvittana* reared on *Prunus* and on *Griselinia*. Cultures were maintained for over five months until a sufficient number of second-generation larvae could be used for the experiment.

6.3.3. Experiments

The experiment was set up in February 2019 in a Fitotron® SGR 'Walk-in' plant growth room under the same controlled environmental conditions used to maintain the cultures of *C. pronubana* and *E. postvittana*. The experiment consisted of two factors, the "pre-treatment" culture (the larval parental diet of either *Griselinia* or *Prunus*) and the "treatment" culture (larval diet of *Prunus, Choisya* or *Griselinia*). Each treatment consisted of six replicates. Treatments were laid out using a Latin Square design (Fisher, 1925). Each species of moth was subjected to the same type of treatment at the same time. Throughout the whole experiment species of moth were isolated from each other. Plants were stood on a black plastic tray and were watered as required from beneath. The height of the plants varied from 20 to 25 cm, and their mid-width measured approximately 12 cm.

Five neonate larvae were collected from each culture and placed on top of each plant using a fine paintbrush, after which the plants were covered with a nylon mesh sleeve (43 cm long by 13 cm diameter; mesh aperture area = 16 qm^2 (1.6×10^{-5} metre), with the open area of a mesh (A^o) = 50%), closed at the top and the bottom in order to isolate plants from each other. Larvae were left undisturbed on each plant to complete their development, recording the time to pupation.

Once each larva had pupated, the pupa was collected and measured after the integument hardened and turned brown. After measurements, pupae were transferred separately to Petri dishes (90 mm diameter x 15 mm height), and placed in the same room under the same constant environmental conditions. Each Petri dish had a circular piece of dry plain white paper towel placed on the bottom of the dish.

Once the adults had emerged, measurements were taken between 6–12 hours after emergence from pupa. Sex was determined using a Microtec HM-3® stereo microscope (TEC Microscopes, UK). One female moth was placed into one clear Petri dish and were allowed to mate with three introduced males (Knight, 2014) that came from the same host plant species as the female. Each female was allowed to lay eggs on the inside walls of the dish up to its death; during this period eggs were counted every 48h using a Microtec HM-3® stereo microscope.

The following variables were recorded: (1) the cumulative duration of larval stage from hatching to pupa formation (until chrysalis was formed), (2) weight of the pupa, (3) date of adult emergence, its sex and weight, (4) total number of eggs and clutches laid per larval host plant species.

6.3.4. Statistical analysis

All statistical tests were performed using R version 4.0.2 (R Core Team, 2020), and the significance level was set at $\alpha=0.05$. The analyses were used to measure the effect of a host plant on the performance of two moth species, each of different feeding-regime background, determining the differences between the life history parameters between and within the moth species. When data did not meet normality (Shapiro-Wilk test) or homogeneity of variances assumptions (Levene’s test), non-parametric tests were used as follows: performance comparison between *C. pronubana* and *E. postvittana*, as well as between two moth cultures, Unpaired Two-Samples Wilcoxon test was used (Mann-Whitney test). Further analyses were performed with the Kruskal-Wallis test, and the Wilcoxon test was used for *post hoc* pairwise comparisons (with P-values adjusted by Benjamini and Hochberg (BH) method).

6.4. Results

6.4.1. Overall differences between *C. pronubana* and *E. postvittana*

Larval survivorship between the two moth species did not differ significantly (Wilcoxon rank sum test: W = 685.5, P = 0.665) with the mean survival for both moths of 3.58 ± 0.14 (71.6%) larvae survived out of the total of five larvae per each host plant applied initially. Host plants significantly affected duration of the larval stage of these two moths, indicating significant difference between longer larval duration of (±SEM) 70.65 ± 2.07 days for *C. pronubana*, and shorter of 46.01 ± 1.20 days for *E. postvittana* larvae (W = 13150, P < 0.0001). Shorter duration produced significantly heavier pupae (31.59 ± 0.97 mg) than the longer larval duration (23.50 ± 1.03 mg) (W = 4300, P < 0.0001). The overall ratio for both moths of total eggs laid between *Prunus*, *Choisya* and *Griselinia* was 3.2 : 1 : 1.9. The highest number of eggs was laid by *C. pronubana* (117 eggs per female in total) with the mean number of 16.30 ± 1.64 eggs laid per clutch. This was significantly higher than the number of eggs laid by *E. postvittana* (68 eggs per female in total) resulting in 21.31 ± 1.98 eggs laid per clutch (W = 26540, P < 0.0001) (Figure 6.1, Table 6.1).

6.4.2. Differences between *C. pronubana* and *E. postvittana* cultures originating from *Prunus*

Overall, for larvae originating form *Prunus* culture (*Prunus* pre-treatment) there was no significant difference in survivorship between *C. pronubana* and *E. postvittana* larvae developing on three host plant species (Wilcoxon test: W = 149, P = 0.6745). A significant difference, however, was observed in larval duration between two moth species (Wilcoxon: W = 4142, P < 0.0001), with 67.68 ± 3.10 days for *C. pronubana*, and 41.50 ± 1.32 days for *E. postvittana*. Weight of pupa also differed between the moths (W = 1318.5, P < 0.0001) resulting in the smaller size pupae for *C. pronubana* (25.02 ± 1.58 mg) and heavier for *E. postvittana* (33.87 ± 1.32 mg). Fecundity did differ here between moths (W = 9258, P = 0.002), with 19.29 ± 3.00 eggs laid per clutch by *C. pronubana*, and 22.85 ± 2.50 eggs per clutch laid by *E. postvittana* (Figure 6.1, Table 6.1).

6.4.3. Differences between *C. pronubana* and *E. postvittana* cultures originating from *Griselinia*

Survivorship for larvae originating from *Griselinia* culture (*Griselinia* pre-treatment), between both moth species did not differ significantly (Wilcoxon: = 193.5, P = 0.3103). Larval duration, however, was significantly longer for *C. pronubana* (74 ± 2.45), than for *E. postvittana* (52.20 ± 1.89) (W = 2591.5, P < 0.0001). Pupal weight differed between species (W = 882.5, P < 0.0001) with 21.78 ± 1.24 mg for *C. pronubana*, and 28.46 ± 1.30 mg for *E. postvittana*. Fecundity in terms of a size clutch also differed significantly between the two moths (W = 3929.5, P = 0.0005) with 13.49 ± 1.48 eggs laid by *C. pronubana*, and 17.92 ± 3.10 eggs laid by *E. postvittana* (Figure 6.1, Table 6.1).

6.4.4. Differences between *Prunus* pre-treatment and *Griselinia* pre-treatment

Moth species originating from two different cultures differed significantly across all four attributes measured here. These can be observed for either for *C. pronubana* larvae developing on *Prunus*, *Choisya* and *Griselinia*, as well for *E. postvittana* larvae (Figure 6.1, Table 6.1).

For *C. pronubana*, there was an overall difference between the two different moth cultures (pre-treatments). *Prunus* pre-treatment affected offspring generation resulting in higher survivorship rate (3.94 ± 0.22) than *Griselinia* pre-treatment. There was a longer larval duration observed for offspring affected by *Griselinia* pre-treatment (74.02 ± 2.45 days) than for *Prunus* pre-treatment (67.68 ± 3.10 days) with 6.34 days difference. Shorter larval duration produced heavier pupae (Pr-culture) (25.02 ± 1.58 mg), and it was 3.24 mg heavier than pupae produced by *C. pronubana* affected by *Griselinia* pre-treatment (21.78 ± 1.23 mg). There was a significant difference between pre-treatments in fecundity. Female offsprings pre-treated with *Prunus* laid on average 5.7 more eggs per clutch (19.29 ± 3.00) than female offsprings pre-treated with *Griselinia* (13.49 ± 1.48).

For *E. postvittana*, *Prunus* pre-treatment displayed significantly higher survival rate (3.94 ± 0.30) than *Griselinia* pre-treatment (3.06 ± 0.26). Significantly shorted larval duration for

Table 6.1. Performance of life history parameters for *C. pronubana* (CTM) and *E. postvittana* (LBAM) and the differences between the parameters are presented between two species of moth, between two moth cultures (pre-treatments) - *Prunus* and *Griselinia* (mean±SEM), and between offspring diet (treatments) - *Prunus* (P), *Choisya* (C) and *Griselinia* (G). General model for either of the moth is detailed in Table 6.2. All data were performed using Kruskal-Wallis rank sum test and pairwise comparison using Wilcoxon rank sum test with continuity correction.

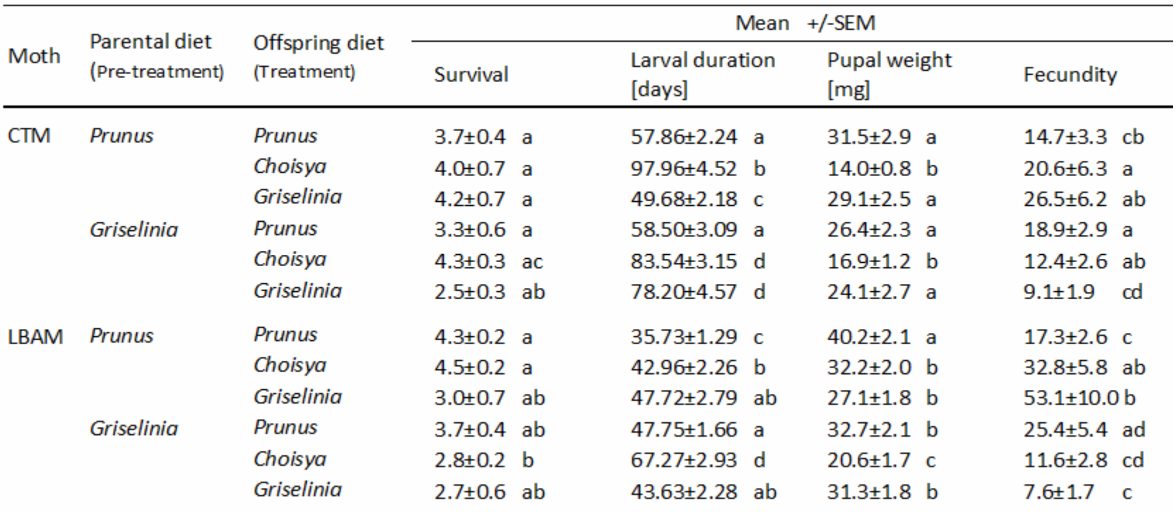
			Survival				Larval duration [days]				Pupal weight [mg]				Fecundity			
Moth	Parental diet (pre-treatment)	Offspring diet (treatment)	Mean +/-SEM	χ2	Df	P-value	Mean +/-SEM	χ2	Df	P-value	Mean +/-SEM	χ2	Df	P-value	Mean +/-SEM	χ2	Df	P-value
Moths	General model CTM-LBAM	PCG	3.6±0.1	25.75	11	0.0071	58.77±1.42	170.37	11	< 0.0001	27.4±0.8	106.87	11	< 0.0001	17.7±1.3	74.87	11	< 0.0001
	CTM-LBAM	P	3.8±0.2	1.32	1	0.25	49.17±1.46	38.04	1	< 0.0001	33.0±1.3	8.55	1	0.004	17.4±1.7	5.61	1	0.018
	CTM-LBAM	C	3.9±0.2	1.79	1	0.18	72.51±2.80	49.64	1	< 0.0001	21.3±1.1	36.06	1	< 0.0001	17.5±2.2	5.75	1	0.017
	CTM-LBAM	G	3.1±0.3	0.69	1	0.41	53.68±2.04	13.03	1	0.0003	28.1±1.2	2.31	1	0.13	18.3±2.9	11.08	1	0.0009
CTM																		
	General model (*Prunus-Griselinia*)	PCG	3.7±0.2	11.51	5	0.042	70.65±2.02	78.16	5	< 0.0001	23.3±1.0	48.9	5	< 0.0001	16.3±1.6	33.96	5	< 0.0001
	Prunus	PCG	3.9±0.2	0.74	2	0.693	67.68±3.10	40.53	2	< 0.0001	25.0±1.6	29.43	2	< 0.0001	19.3±3.0	9.21	2	0.009
	Griselinia	PCG	3.4±0.3	9.77	2	0.011	74.02±2.45	23.51	2	< 0.0001	21.8±1.2	12.58	2	0.002	13.5±1.5	25.41	2	< 0.0001
	Prunus-Griselinia	P	3.5±0.3	0.18	1	0.675	58.17±1.86	0.05	1	0.82	28.9±1.9	2.21	1	0.137	16.4±2.3	8.00	1	0.005
	Prunus-Griselinia	C	4.2±0.2	0.49	1	0.484	90.15±2.85	8.11	1	0.004	15.7±0.8	2.71	1	0.1	14.0±2.5	2.64	1	0.104
	Prunus-Griselinia	G	3.3±0.4	5.82	1	0.016	60.38±3.09	21.43	1	< 0.0001	27.2±1.9	1.48	1	0.224	17.1±3.1	13.58	1	0.0002
LBAM																		
	General model (*Prunus-Griselinia*)	PCG	3.5±0.2	13.42	5	0.0197	46.01±1.20	49.76	5	< 0.0001	31.6±1.0	38.3	5	< 0.0001	21.3±2.0	24.79	5	< 0.0002
	Prunus	PCG	3.9±0.3	4.17	2	0.125	41.50±1.32	14.36	2	0.0008	33.9±1.3	17.03	2	0.0002	22.9±2.5	18.26	2	< 0.0001
	Griselinia	PCG	3.1±0.3	3.02	2	0.221	52.20±1.85	26.33	2	< 0.0001	28.5±1.3	18.32	2	0.0001	17.9±3.1	6.12	2	0.047
	Prunus-Griselinia	P	4.0±0.3	1.59	1	0.207	40.96±1.35	19.15	1	< 0.0001	36.7±1.6	8.37	1	0.004	19.3±2.4	4.84	1	0.028
	Prunus-Griselinia	C	3.7±0.3	9.21	1	0.002	51.85±2.56	18.52	1	< 0.0001	28.0±1.7	12.67	1	0.0004	24.0±4.0	5.93	1	0.015
	Prunus-Griselinia	G	2.8±0.5	0.24	1	0.622	45.79±1.83	0.69	1	0.407	29.1±1.3	2.52	1	0.113	28.1±6.8	11.48	1	0.0007

Prunus pre-treatment (41. 50 ± 1.32 days) of 10.7 days, than duration for *Griselinia* pre-treatment (52.20 ± 1.85 days), produced 5.41 mg heavier pupae (33.87 ± 1.32 mg) than *Griselinia* pre-treatment (28.46 ± 1.30 mg), of which larvae were developing longer (52.20 ± 1.85 days). Heavier pupae tended in producing adult females (*Prunus* pre-treatment), laying 3.88 more eggs per clutch (21.80 ± 3.06) than moths originating from *Griselinia* culture (17.92 ± 3.10). It was observed that under natural conditions, *E. postvittana* can lay on average 35.00 ± 0.80 eggs (Danthanarayana, 1983).

6.4.5. *Cacoecimorpha pronubana* – differences between pre-treatments on three host plant species

Performance of this tortricid species was compared between *Prunus* and *Griselinia* pre-treatments on three hosts (treatments) – *Prunus, Choisya* and *Griselinia* (Table 6.1 and 6.2). No significant differences in survivorship between two pre-treatments was observed on any of the host, however, differences were recorded in duration of larval stage on *Griselinia* and *Choisya*. There were no differences between both pre-treatments in pupal weight on any of the hosts, however, fecundity, in terms of a clutch size, differed significantly between pre-treatments when offspring larvae developed on *Prunus* and *Griselinia* host plants (treatments).

Table 6.2. Performance of life history parameters is represented for *C. pronubana* (CTM) and *E. postvittana* (LBAM), originated from cultures (pre-treatments): *Prunus*, and *Griselinia* as larval parental diets, and between host plant species as larval offspring diet (treatment) – *Prunus*, *Choisya* and *Griselinia* on which larvae were developing during the experiment (mean ± SEM). This table is an extension for 'General model' for either of the moth found in Table 6.1. Fecundity is represented here in the mean number of eggs laid per clutch. Lowercase letters represent statistical differences between different offspring diets (treatments) for each individual moth species, as a result of *post hoc* pairwise comparisons Wilcoxon test (with P-values adjusted by Benjamini and Hochberg (BH) method).



Moth	Parental diet (Pre-treatment)	Offspring diet (Treatment)	Mean +/-SEM			
			Survival	Larval duration [days]	Pupal weight [mg]	Fecundity
CTM	*Prunus*	*Prunus*	3.7±0.4 a	57.86±2.24 a	31.5±2.9 a	14.7±3.3 cb
		Choisya	4.0±0.7 a	97.96±4.52 b	14.0±0.8 b	20.6±6.3 a
		Griselinia	4.2±0.7 a	49.68±2.18 c	29.1±2.5 a	26.5±6.2 ab
	Griselinia	*Prunus*	3.3±0.6 a	58.50±3.09 a	26.4±2.3 a	18.9±2.9 a
		Choisya	4.3±0.3 ac	83.54±3.15 d	16.9±1.2 b	12.4±2.6 ab
		Griselinia	2.5±0.3 ab	78.20±4.57 d	24.1±2.7 a	9.1±1.9 cd
LBAM	*Prunus*	*Prunus*	4.3±0.2 a	35.73±1.29 c	40.2±2.1 a	17.3±2.6 c
		Choisya	4.5±0.2 a	42.96±2.26 b	32.2±2.0 b	32.8±5.8 ab
		Griselinia	3.0±0.7 ab	47.72±2.79 ab	27.1±1.8 b	53.1±10.0 b
	Griselinia	*Prunus*	3.7±0.4 ab	47.75±1.66 a	32.7±2.1 b	25.4±5.4 ad
		Choisya	2.8±0.2 b	67.27±2.93 d	20.6±1.7 c	11.6±2.8 cd
		Griselinia	2.7±0.6 ab	43.63±2.28 ab	31.3±1.8 b	7.6±1.7 c

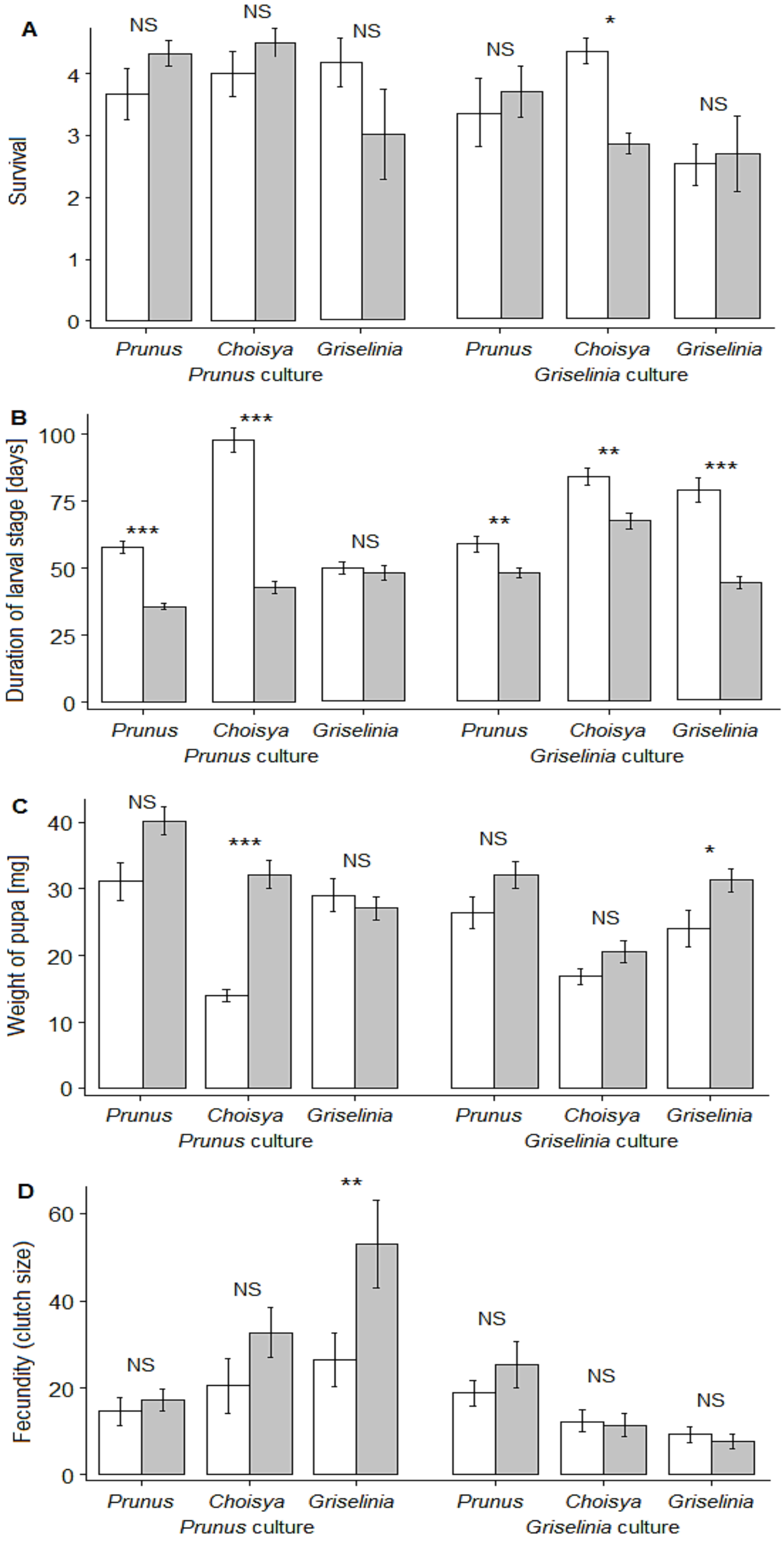


Figure 6.1. Comparisons of four life history traits between two moths, *C. pronubana* (white bars) and *E. postvittana* (grey bars) reared on three larval diets (treatment) – *Prunus*, *Choisya*, *Griselinia* (mean ± SEM). Three white or three grey bars at the left of the plots represent larvae originating from *Prunus* culture (pre-treatment), and three bars at the right, from *Griselinia* culture (pre-treatment). Comparisons between moth species was performed with Kruskal-Wallis test, NS P > 0.05, * P < 0.05, ** P < 0.01, *** P < 0.0001. Uppercase letters in the top left corner of each graph represent as follows: A – survival, B – duration of larval stage in days, C – weight of pupa in milligrams, D – fecundity is represented in number of eggs laid per clutch.

6.4.6. *Epiphyas postvittana* – differences between pre-treatments on three host plant species

For both pre-treatments, only *Choisya* affected differently survivorship of *E. postvittana* offspring larvae. Larval duration and pupal weight, however, was affected differently by *Prunus* and *Choisya* between both pre-treatments. The size of clutches differed significantly on all three host plant treatments. *Prunus* pre-treatment affected offspring larvae developing on each of the host plant treatments – *Prunus, Choisya* and *Griselinia*, and this was different to how treatments affected offspring larvae that originated from *Griselinia* culture (Table 6.1 and 6.2).

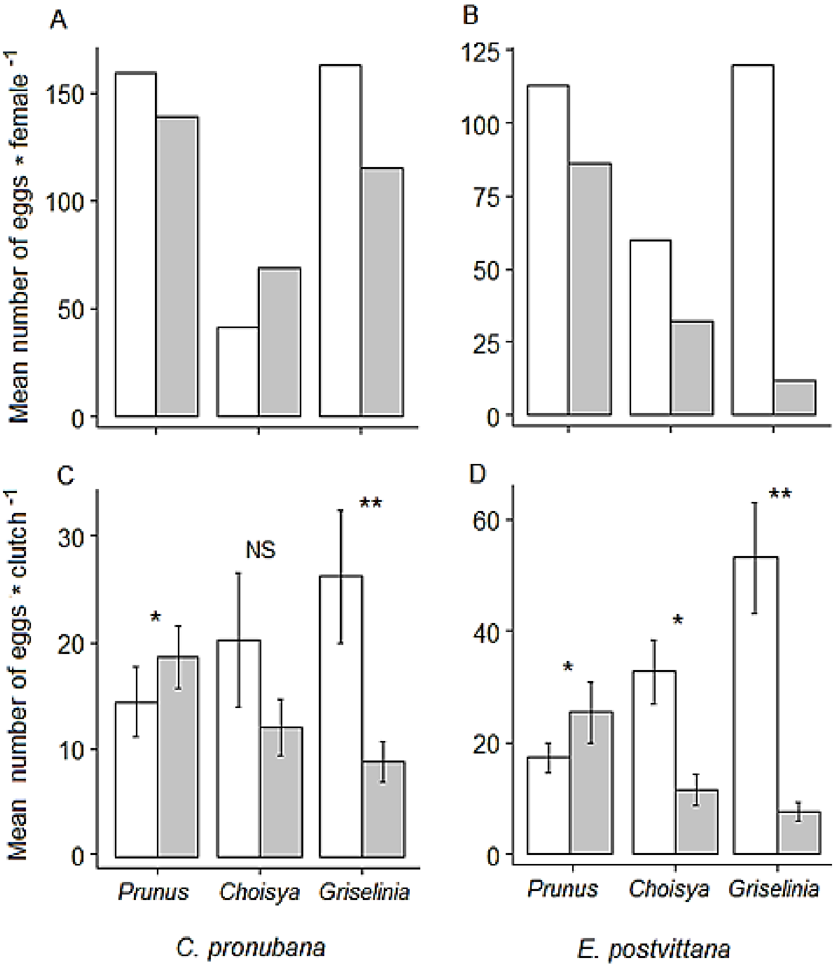


Figure 6.2. Comparisons of fecundity on three different host plant species is represented in mean number of eggs laid per female (A, B), and in mean number of eggs laid per clutch (C, D) for *C. pronubana* (left) and *E. postvittana* (right) between *Prunus* cultures (pre-treatment) (white bars), and *Griselinia* cultures (pre-treatment) (grey bars) (mean ± SEM). Comparisons between cultures (pre-treatments) for each host plant were performed using Wilcoxon rank sum test with continuity correction, NS P > 0.05, * P < 0.05, ** P < 0.01, *** P < 0.0001.

6.5. Discussion

The results from this study demonstrate the effect of diet on four history traits of two moth species, *C. pronubana* and *E. postvitanna*, originating from two different feeding regimes – *Prunus* (Rosaceae) and *Griselinia* (Griseliniaceae). Overall, the moth species exhibited significant differences between their life history traits, except larval survivorship. The shortest duration of larval stage from egg hatching to pupal formation produced heavier pupae resulting in larger clutch sizes, which is a common phenomenon in Lepidopterans (Barbosa and Capinera, 1977; Rossiter, 1991; Yu *et al.,* 2016). It is possible that the differences in performance between these two moths reflect different utilisation abilities of the larva on the same host (Roslin and Salminen, 2008), or development strategies of a larva in order to increase its survivorship (Damman, 1987; Abarca *et al.,* 2014). It is known that prolonged development may be an important factor that determines survival by the exposure of a larva to predators and parasitoids (Thiery and Moreau, 2005), however, this may significantly vary across Lepidopteran species. The parasitism rate of *Cotesia glomerata* (Linnaeus, 1758) (Hymenoptera: Braconidae), for example, on the larvae of the cabbage butterfly, *Pieris rapae* (Linnaeus, 1758) (Lepidoptera: Pieridae), significantly increased on *Brassica oleracea* L. (Brassicales: Brassicaceae), the plant species on which *P. rapae* developed most rapidly (Benrey and Denno, 1997).

Overall, three host plant species – *Prunus* (Rosaceae), *Choisya* (Rutaceae) and *Griselinia* (Griseliniaceae) also affected the moths' performance differently, although, development patterns between larval duration, pupal weight and fecundity remained largely the same. Host plants, however, affected *C. pronubana* and *E. postvittana* female adults originating from two independent cultures. The change in diet resulted in significant shift in female oviposition behaviour for both species. From the results of this study it was observed that fecundity in terms of a clutch size differed significantly; larvae that originated from *Prunus* culture and developing on *Griselinia*, produced adult females that produced larger clutch sizes than larvae originating from *Griselinia*. The same scenario was observed in this study for larvae originating from *Griselinia* culture, but developing on *Prunus.* It is possible that the information about the physiochemical characteristics of the host plant on which larvae were developing, remained through the metamorphosis and was reflected by the ovipositional behaviour of the female adults (Anderson *et al.,* 2013; Petit *et al.,* 2015; Proffit *et al.,* 2015). It was hypothesised that the leaf size or shape, resource abundance or olfactory cues may not be the only determinant of a clutch size or oviposition behaviour found in this study for an adult female, as it was shown for other Lepidopterans (Kagata and Ohgushi, 2002; Stefanescu *et al.,* 2006; Rizvi and Raman, 2015; Dell'Aglio *et al.,* 2016). It is possible, however, that the female adopted different trade-off strategic approach and responded by producing smaller size clutches on the already known host plant, with the opposite response to the unknown host. As it was shown for some other

Lepidopterans, greater size clutches (or other type of an attribute) are tend to be less parasitized, than smaller size (Beckage and Riddiford, 1983; Geervliet *et al.,* 1998; Stuart and Polavarapu, 2000; Randlkofer *et al.,* 2007). Despite the theory, that clutch size is determined by the availability of life-supporting resources (Godfray *et al.,* 1991), perhaps such behaviour reflected one of the selective pressures necessary for neonates to build an effective shelter in response to natural enemies along with initial food availability (Damman, 1987).

Significant change in fecundity as a response to the sudden change of diet to which the larvae were exposed, may reflect phenotypic plasticity of these two polyphagous species' ovipositional behaviour. It is possible, that such behaviour governs their population dynamics in natural habitats (Thöming *et al.,* 2013). Similar inter-population variations were found for *E. postvittana* that were related to climatic differences. It was shown, that populations from warmer regions develop more slowly, producing smaller and less fecund females but with a stronger flight capacity, than those from cooler climates (Gu and Danthanarayana, 2000). It is possible that sudden changes in certain characteristics of a host plant experienced by a larva may influence the phenotypic plasticity of the adult female. Such response may be a form of a spatial distribution or exploration strategy to a new unknown habitat, or as a response to new patterns within the habitat in terms of egg survival strategy and their protection against predators (Görür, 2005; Fusco and Minelli, 2010). It is unclear, however, how dietary changes experienced by a single genotype in this study can affect a complex phenotypic plasticity across various traits of these two moth species, either within-generation phenotypic plasticity, or through transgenerational phenotypic plasticity across different tortricid species (Fox and Mousseau, 1998; Rösvik *et al.,* 2020).

The results illustrate that the parental host plant can influence life history variation in progeny transgenerationally in complex ways. Two herbivore species presented in this study differ, and transgenerational feeding regime did affect life history parameters of these two moths. Although, moths do exhibit similar patterns in their life history traits, it was shown that their performance can be affected differently by different host plant at different stages of their life cycle. Results presented here on oviposition behaviour, however, may be a common trait for these two pests. This might be an important natural mechanism that control the species' local migrations and the degree at which they may affect a crop environment. This suggests a role for changes in, for example, management of plant diversity in crop habitats as a strategy for pest control where planned, sequential changes in host plant species could be designed to target multiple generations of the same insect pest. However, the mechanisms underlying physiological changes in insect performance through transgenerational dietary changes are still unclear.

Chapter 7. General discussion

In this chapter life history traits of two species of moth, the carnation tortrix moth, *Cacoecimorpha pronubana*, and the light brown apple moth, *Epiphyas postvittana* are discussed in light of integrated pest management, in response to the aims and objectives formulated in this thesis.

7.1 The moths

The carnation tortrix moth, *Cacoecimorpha pronubana* (Hübner, [1799]) and the light brown apple moth, *Epiphyas postvittana* (Lepidoptera: Tortricidae) (Walker, 1863) are economically important pest species (Kacar and Ulusoy, 2008; Brockerhoff *et al.,* 2011; Pencheva and Yovkova, 2016; Reddy, 2016). In Britain both moths produce two generations per year (Fisher, 1924; Suckling and Brockerhoff, 2010). They are highly polyphagous species, together affecting over 500 plant species that belong mainly to the families Asteraceae, Fabaceae, Oleaceae, Rosaceae, Rutaceae, Solanaceae (Beitia *et al.,* 2016; CABI, 2020) and Griseliniaceae (personal observation). The fragile balance of insect communities and microbial diversity within a crop environment is often exposed to synthetic pesticides that are used to control these pests (Gullino and Wardlow 1999; Sterk *et al.,* 1999; Biondia *et al.,* 2012). A detrimental impact that synthetic pesticides have had on the biocenosis over the past decades led to the emergence of alternative strategies of pest control, simultaneously laying foundations for the adoption of integrated pest management practices as an effective solution to control pests (Copping and Menn, 2000; Van Lenteren, 2000).

7.2 An ornamental crop habitat: a complex ecosystem

The life history traits of these two generalist species, such as larval and pupal development, adult fitness, longevity, fecundity and oviposition preferences are all affected by factors that are often difficult to unequivocally identify. An ornamental crop habitat is a complex agroecosystem that is composed of a wide range of plant species. Crop plants can be grown unprotected – exposed to natural weather conditions, or under protected arrangements – grown in, e.g., glasshouses or polytunnels. Crop plants are frequently exposed to a number of different biotic and abiotic factors which affect plants' health and performance. Herbivorous pests, plant pathogens, weather, growing conditions (e.g. pots, growing medium, water quality), pesticides or other cultural controls, are components that often affect the crops, and their habitats. Constant changes within such agroecosystem create microclimates, and microhabitats that often are not permanent entities. Growers, therefore, should rely on a combination of comprehensive information on the life cycle of the pests and their interaction with a crop habitat (Dhawan and Peshin, 2009). Such an approach should aim at incorporating aspects of attracting natural enemies within a crop environment along with the use of suitable biological control agents (Van Lenteren, 2002) and the use of practices that promote higher plant diversity that enhances the activity of beneficial organisms (Sanguankeo and Leon, 2011). When implementing novel methods within IPM programmes, it is important to note that fitness of the moths is maintained naturally within a commercial ornamental nursery through the diverse range of plant species grown. A number of studies have shown that herbivorous insects typically perform better when presented with diets comprised of a range of different plant species, e.g., butterflies and moths (Merz, 1959; Hägele and Rowell-Rahier, 1999), grasshoppers (Barnes, 1955; Chandra and Williams, 1983) and crane flies (Hägele and Rowell-Rahier, 1999). This may be due to maintenance of nutritional balance (Pulliam, 1975; Rapport, 1980), or the dilution of allelochemicals contained in the food plants (Freeland and Janzen, 1974). Perhaps abundance and population dynamics of a pest within a crop environment may reflect the diverse range of host plant species available within this environment. This may explain here the results from the study (Chapter 6) on the effect of different host plant species through transgenerational dietary changes on the performance of these two species of moth. The change in diet resulted in significant shift in female oviposition behaviour for both species, which may imply, that such behaviour governs their population dynamics in natural habitats (Thöming *et al.,* 2013). It is possible that dietary changes experienced by a larva may influence the phenotypic plasticity of the adult female, and such response may be a form of a spatial distribution or exploration strategy to a new habitat in terms of egg survival strategy, e.g., against predators (Görür, 2005; Fusco and Minelli, 2010). Oviposition behaviour in Lepidopterans may be also affected by plant volatile compounds which are known to be important olfactory cues (Leather, 1995; Witzgall *et al.,* 2005. Markheiser *et al.,* 2020). Oviposition preference, however, may also be governed by the physical characteristics of the surface on which eggs are deposited (Hagley *et al.,* 1980; Tomkins *et al.,* 1991). Although, surface texture may be an important factor determining the oviposition behaviour of the adult female (Foster *et al.,* 1997), yet, denser foliage may encourage female moths to oviposit more eggs (Foster *et al.,* 1997; Wearing, 1998). Chemical signals generated by plants often carry information about plant quality, such as plant age, growth rate, nutritional status or damage caused by herbivorous insects (Awmack and Leather, 2002; McCallum *et al.,* 2011). These chemical cues emited by the host plant are used by the neonate larvae to identify a suitable feeding site; however, they will also encounter many challenges while exploring the surrounding area, e.g., natural enemies, or unfavourable weather conditions (Castrejon *et al.,* 2006). Nutritional value of a plant, such as higher nitrogen content, often accelerates larval development (Lindroth *et al.,* 1997) increasing the size and the reproductive performance of an adult moth, as it was shown for European grapevine moth, *Lobesia botrana* ([Denis and Schiffermüller, 1775]) (Thiery and Moreau, 2005). Plant chemical defence responses, on the contrary, may prevent or inhibit feeding of the larva (Roth *et al.,* 1997; Chen, 2008), or emit volatile compounds (VOC) attracting natural enemies of the herbivore (Du *et al.,* 1998. Dudareva *et al.,* 2004; War *et al.,* 2012). It is, therefore, very important for the larva to choose a host plant that would guarantee building an effective shelter against predators. Immature foliage may not always be the best shelter-material, but it tends to be more nutritious and easier to digest for the neonates, still, despite the highest content of defence compounds (Moreira *et al.,* 2016). Such larvae may perhaps use the less nutritious, more mature or senescent foliage later, where they could develop and emerge as an adult (Bittencourt-Rodrigues and Zucoloto, 2009).

7.3 Monitoring of *Cacoecimorpha pronubana* and *Epiphyas postvittana*

Monitoring insect populations is probably one of the most important and fundamental components of every IPM programme suppling growers with information needed to control pest populations effectively. The result from this study on the abundance and phenology of adult males in the commercial ornamental plant nursery, proved that these pests are active and present each year. Personal observations also confirmed that both pests can cause significant damage to a wide range of ornamental plant species. The monitoring of the pests in this study was initially completed through monitoring the pest populations using pheromone traps; open-sided delta traps baited with a synthetic female sex pheromone lure. Unquestionably, the monitoring of pest populations may be also useful for other insect species that are present within a crop habitat, especially those that potentially interact with or affect pest species populations, i.e. natural enemies or predators. Monitoring natural enemies or predators of the pests within an agroecosystem, however, may be more difficult than monitoring only pest population. At the present time, there may be few, if any, consistently effective synthetic pheromones for monitoring hymenopteran parasitoids. Almost certainly, however, efficient monitoring methods may need to be developed, or improved if such already exist (Keeling *et al.,* 2004). While previous attempts to determine population dynamics of a pupal parasitoid, *Diapetimorpha introita* (Cresson) (Hymenoptera: Ichneumonidae) have relied upon measuring frequency of parasitism among fall armyworm pupae in the field, new approaches, such as pheromone wing traps baited with live females to catch *D. introita* males for monitoring the seasonal abundance of *D. introita*, proved to be also effective (Jewett and Carpenter, 2001).

It was observed in this study that abundance of *E. postvittana* adult males caught, was significantly higher to the abundance of *C. pronubana* adult males. Interestingly, however, the seasonal abundance for *C. pronubana* differed significantly between seasons throughout the five-year study period, and the seasonal abundance for *E. postvittana* did not differ significantly between these years. Such information gives an interesting new insight into the dynamics of these two populations of moth, and may possibly generate novel approaches when monitoring insect populations within a crop, e.g., monitoring or identifying natural enemies that may influence the abundance or phenology of the pest population, or manipulating temperature, humidity or sunlight in order to affect life history traits of the pests for the benefit of a grower. Previous research has suggested that *E. postvittana* is a relatively abundant, cosmopolitan pest species (Suckling *et al.,* 1985; Fountain and Cross, 2007; Suckling *et al.,* 2014) with significant potential for becoming established in new habitats (He *et al.,* 2012). The abundance of *C. pronubana* populations, however, remains well established in known habitats (Cavalloro, 1986; Leandro *et al.,* 2002; Brown *et al.,* 2010). Indeed, differences observed between years in seasonal abundance of *C. pronubana*, may be characterised by inter-seasonal variations in phenological patterns reflected by the species susceptibility to certain environmental changes (e.g., weather conditions, host plant habitats). It appears, however, that abundance of *E. postvittana* populations are more uniform between years, and perhaps this indicates that species is better adapted to withstand changes within different crop habitats (Kingsolver, 1989; Kiritani, 2013; Khaliq *et al.,* 2014). Such phenomenon may agree with the fact that the abundance of *E. postvittana* observed in this study was not affected by the seasonal changes in temperature, precipitation and sunshine duration. On the contrary, however, these factors (except precipitation) affected abundance of *C. pronubana,* a phenomenon known to occur in insects (Taylor, 1963; Solbreck, 1991; Gilbert and Raworth, 1996).

Results from this study suggest that knowledge about life history parameters of these Lepidopteran species may not be sufficient in order to control pest populations effectively. It appears, therefore, that monitoring may be another important key element that should be considered when improving IPM control strategies. Monitoring abundance of pest population and weather conditions may help in identifying and predicting timescales and life stages of the insect present more accurately, leading to improved choices in grower's approach toward control strategies within IPM programmes. Yet, the study (Chapter 2) shows that pests' abundance and phenological patterns differ each year, which indicates, that control approaches may differ too in each coming season.

7.4 Control of *Cacoecimorpha pronubana* and *Epiphyas postvittana*

Control of *C. pronubana* and *E. postvittana* in ornamental plant nursery aims to inhibit or eradicate the pests from the crop mitigating the economic consequences of the potential damage (Barzman *et al.,* 2015). Integrated pest management, however, is a control that is based on predicted economic, ecological and sociological consequences. Such strategy aims to make maximum use of naturally occurring control agents, including weather, crop habitat diversity, predators and natural enemies of a pest or disease (Bottrell and Bottrell, 1979).

7.4.1 Pheromone traps

Apart from monitoring, as described in Chapter 2, pheromone traps are also used to provide mating disruption. It has been successfully employed to reduce pest populations targeting adult males, however, this method has a disadvantage as it reduces populations of non-target species that are occasionally caught in traps. Mating disruption has been generally recognised as a good control strategy, and is being adopted often within IPM programmes. It was shown, however, that although the mating disruption technique can be used to effectively control pest populations, the technique is not as effective at high population densities of a pest (Louis and Schirra, 2001).

7.4.2 Effect of host plants on oviposition preference

Adult females of these two species of moth usually oviposit eggs on the upper surface of leaves in clutches containing typically 1–200 eggs, however, eggs may be oviposited on the other than host plant surfaces as it was showed in Chapter 3. Light green in colour, oval, an egg measure approximately 0.84 by 0.95 mm (Fisher, 1924; Danthanarayana, 1975). The clutches can be visually noticed with a naked eye, without the need for the use of any specialised equipment. Egg count, however, may require a magnifying lens, usually X20. There are many factors that influence oviposition of adult females in the crop habitat, and it is often difficult to predict females' preference in choosing the site to lay eggs. Considering that both species of moth exhibit two generations per year, as it was showed in Chapter 2, a grower may be able to predict and determine times at which adult females appear and begin to lay eggs. The economic threshold for both species of moth is a catch of over 30 adult male moths caught per pheromone trap per week (AHDB, 2020). Pest management practices initiated by growers should be made regardless of the plant growth stage. Such approach should allow for the choice of the most suitable control strategy. As it was shown in Chapter 2, oviposition preference of *C. pronubana* and *E. postvittana* may not be solely governed by the chemical properties of the plants, but also the physical characteristics of the surface on which eggs are deposited (Hagley *et al.,* 1980; Tomkins *et al.,* 1991). It is possible that surface texture is an important factor determining the oviposition behaviour of the females with the preference to lay eggs on smoother surfaces rather than on the rougher (Foster *et al.,* 1997). It was also shown, that adult female of *C. pronubana* can lay over four times more eggs on glass and wooden structures of a glasshouse, than on a plant foliage (Burges and Jarrett, 1976). Understanding where eggs are likely to be laid (e.g., artificial surfaces or host plants), may contribute to monitoring and controlling pest populations better within an IPM programme. Such a strategy may be especially beneficial in protected crops grown, e.g., in glasshouses, or polytunnels. Control efforts, therefore, may initially implement the monitoring of artificial surfaces for the presence of eggs. Another study showed that moths can also use visual cues to choose the oviposition site, such as colour (Foster *et al.,* 1997). Therefore, establishing smooth artificial surfaces, possibly coloured, on which female adults would be encouraged to deposit eggs, may be an additional strategy to control these pests. It is unclear, however, why the oviposition preferences showed in this study included significant amount of eggs laid on artificial surface. It is possible, that female moths tend to choose to oviposit on different plant species, perhaps expanding a range of host plant species that may potentially be suitable for her offspring.

In addition to the above, some authors showed that denser foliage tends to encourage the moth to oviposit more eggs, which was also true for *E. postvittana* (Foster *et al.,* 1997; Wearing, 1998). Result from Chapter 4, 5, and 6 suggest that information about foliage density or/and the size of leaves of host plants on which larvae would develop may retain through the metamorphosis and affect the adult female fecundity in terms of the size of egg clutches. This phenomenon may be a form of adaptation in terms of a host plant exploitation by the larvae (Davies and Gilbert, 1985). Brown and Cameron (1979), for example, showed that there is a strong correlation between decreased size of egg clutches and increased parasitism on the Gypsy moth, *Lymantria dispar dispar* (Linnaeus, 1758) eggs.

Such a phenomenon may suggest, that crop habitat density is an important determinant of the females' oviposition strategy, and may be considered as a preventative control measure before establishing a crop plant within a specified area. Perhaps manipulating the density of the crop plants grown within a designated area may benefit the crop habitat.

7.4.3 Effect of host plants on life history parameters

Understanding how host plants affect life history traits of insect pests in crop habitats should be of high importance to the grower, but also to entomologists and scientists that aim to improve the knowledge of these pests, strengthening foundations towards improving crop protection methods employed within IPM programmes. As it was shown in this study (Chapter 4, 5 and 6), host plant suitability plays an important role in shaping the feeding behaviour of a larva and determine the larval and adult performance in terms of its longevity, body size, fecundity and mating and ovipositional behaviour (Brewer *et al.,* 1985; Lance, 2012; Moreau *et al.,* 2017). The quality of a prey reflected by the host plants, therefore, subsequently determines performance of natural enemies (Kacar and Ulusoy, 2012; Feng *et al.,* 2015; Yazdani, 2015). The presence of tortricid larvae in the crop habitat should be of concern to the grower, as this is the only stage within a life cycle of the pest that damages a plant. After hatching, the larva disperses immediately in search for a suitable feeding site. It produces silken thread that it uses for relocating around the crop habitat. The thread is also used for constructing a shelter typically by rolling leaves together (Lo *et al.,* 2000). Such plant damage can be visually noticed without any effort. The larvae of these pests may be controlled by, for example, organophosphate insecticides, although, a growing reluctance among growers concerned with its toxicity increases an interest in the use of alternative, less harmful control methods (Bailey *et al.,* 1996). The control of these pest within IPM programmes usually involves the use of microbial agent – pathogenic bacteria, *Bacillus thuringiensis* (Burges and Jarrett, 1976; Cross *et al.,* 2001), or the use of natural enemies or predators, such as braconid wasps, or other species belonging to the family Ichneumonidae (Hymenoptera: Ichneumonidae), (Fisher, 1924; Danthanarayana, 1980; Mifsud *et al.,* 2019).

Moth performance is equally likely to be linked to factors such as secondary metabolites, plant nutrients, or mechanical properties of a host plant (Du *et al*., 1998; Colasurdo *et al.,* 2009; War *et al.,* 2012). Results from this study (Chapter 4, 5 and 6) have shown that different ornamental host plant species, do indeed, affect the development of *C. pronubana* and *E. postvittana*. This further suggests that the performance of the moth may reflect the suitability of a host plant for the larva to feed on, both in terms of the nutritional value of the available food, and the ability to build a shelter for the larva to survive (Stockhoff, 1991; Roth *et al.,* 1997; Chen, 2008; Krams *et al.,* 2015). The results from this study also showed that the longer the duration of larval stage, or the less suitable food resources are, the greater the negative impact on the development of the adult moth may be. These results are supported by other studies that indicate that nutritional value of the plant is one of the most important factors in determining, e.g., larval performance or its ability to survive (Ojeda-Avila *et al.,* 2003; Marazzi and Städler, 2004). This implies that determining the nutritional values of the crop plants grown, along with determining host plant suitability through monitoring the length of the duration of the larval stage, may be a promising and important element to consider for improving control strategies within an IPM system.

Parental diet and the offspring diet in this study (Chapter 6) did not affect fecundity (egg clutch size) of the offspring. The transgenerational effect of parental diet, however, had a significant effect on the oviposition of progeny female adult. It is possible, that the transgenerational change in host plant experienced by a larva may influence female ovipositional behavior (Gu and Danthanarayana, 2000; Thöming *et al.,* 2013). Such a response may be a form of a spatial distribution or exploration strategy to new habitat in terms of egg survival (Görür, 2005; Fusco and Minelli, 2010). Despite the theory that clutch size is determined by the availability of resources (Godfray *et al.,* 1991), perhaps production of larger egg clutches reflects one of the selective pressures necessary for neonates to survive, for example, by building an effective shelter in response to natural enemies along with initial food availability (Damman, 1987). It is possible that the parental host plant can influence life history variation in progeny transgenerationally in complex ways. Perhaps manipulation of plant diversity in crop habitats may be a strategy for pest control where planned, sequential changes in host plant species could be designed to target multiple generations of the same pest species.

7.4.4 Summary

Frequent monitoring of trophic interactions within a crop habitat may be an important determinant of population abundance and dynamics, the structure and persistence of insect communities, forecasting models, and an efficient tool for assessing sustainability of the ecosystem processes occurring within ornamental plant nursery (Ings *et al.,* 2009). Further efforts to improve understanding of pest performance may focus on monitoring of the most susceptible host plant species to these pests where larval development is most successful as this in return will affect the performance of the adult moths developing on these host plants (Stockhoff, 1991; Colasurdo *et al.,* 2009; Carrasco *et al.,* 2015). Crop manipulation through diversification practices, such as trap cropping, intercropping, natural enemy refuges, or floral resources for parasitoids and predators, would significantly improve the natural enemies' biodiversity, reduce pest pressure, and increase the yield (Poveda *et al.,* 2008; González-Chang *et al.,* 2019). This may also potentially reduce the local dispersion of the larvae limiting its infestation (Ratnadass *et al.,* 2012). As high diversity of host plant species maintains fitness of herbivorous insects and as a result the highest level of performance (Hägele and Rowell-Rahier, 1999), manipulation and diversification of crop species may require careful consideration. The performance of these two species of moth may be affected not only by certain characteristics of the host plant (Brewer, 1985; Lance, 2012; Moreau *et al.,* 2017), but also by the dietary changes through multiple generations of these species. The role and importance of transgenerational plasticity, however, is not yet entirely understood (Rösvik *et al.,* 2020).

7.5 Conclusion and recommendations for further studies

This study is the first to simultaneously analyse the life history traits of *C. pronubana* and *E. postvittana* within ornamental crop habitats in the UK. In line with the hypothesis of this thesis, the results provide with the knowledge that will help in better understanding of how these two pest species may interact within ornamental crop habitats. A better understanding of the population dynamics and the behaviour of these two Lepidopterans may be useful in developing forecasting models, determining crop specific dynamics or spatial distribution of these pests, as well as in developing more accurate IPM strategies within horticultural crop habitats.

Recommendations for further studies:

1) *In situ* conducting experiments of pest species in relation to experiments conducted in each Chapter of this thesis

2) Determination and clarification of the importance of the type of diet (artificial, single host plant, multiple host plants/diverse) used for the establishment and rearing of the species of moth colonies used for experiments

3) Determination of nutritional value of host plants in relation to life history parameters of the pests. Characteristics of the pupae – a good indicator for *in situ* determination of the larval host plant preference and suitability?

4) Determination of chemical properties (defence and attraction) of host plants in relation to life history parameters of these pests

5) Determination of physical characteristics of the host plant/leaf in relation to oviposition behaviour, and larval feeding behaviour

6) Determination of performance of natural enemies in relation to the quality of prey and the quality of host plant.

7) Host plant density, foliage density and size of leaves in relation to ovipositional behaviour

8) Determination of artificial surfaces/visual stimuli or attractants in relation to ovipositional preference

8) Inter- and intradecadal determination of the abundance and phenology within crop habitats for these pests

9) Determination of intraseasonal (intergenerational) physio-chemical changes within a host plant in relation to feeding behaviour of the larva, including survivorship, preference and performance.

12) Development of pheromone traps for natural enemies and predators of these pests

10) Determination of the abundance and phenology of natural enemies and predators within crop habitats for these pests

11) The role and importance of transgenerational plasticity in relation to diet of these pests

12) Host plant species diversity – intestinal microbiome diversity. Pest preference, performance, and adaptive plasticity.

Author contributions

I, designed, formulated, maintained and conducted all experiments and surveys, collected and maintained data from laboratory experiments, and from the *in situ* moth pheromone traps monitoring. Analysed the results, statistically analysed the data and presented graphically, and wrote each part of each chapter (manuscript) discussing the results. Presented each chapter in the form of manuscript for publication.

Simon Leather and Tom Pope offered me to use entomological laboratories based at Harper Adams University for my experiments providing me with all essential equipment. Both assisted and supported me during formulating experiments and writing this thesis and manuscripts. Both were reviewing my progress during formulating my results and discussions, and writing this thesis.

Edwin Harris supported me with statistical analyses. He contributed as a co-author to two manuscripts reviewing the work, data and analyses. He supported, suggested and incorporated some of the statistical analyses within the manuscripts.

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