

Final Report

June / 2025

Student Project No. CTP-FCR

Title: Studying *Forficula auricularia* and *Eriosoma lanigerum* interactions in apple orchards to better understand their distribution for improved crop protection

Earwigs and woolly apple aphid in dessert apples

Hayden Tempest^{1,2}

¹ Harper Adams University, Centre for Crop and Environmental Science, Agriculture and Environment Department, Newport, Shropshire, TF10 8NB, UK

² Niab, New Road, East Malling, Kent, ME19 6BJ, UK

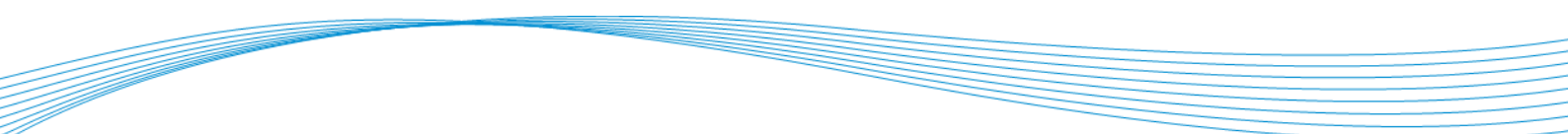
Supervisors: Tom Pope, Michelle Fountain, Ed Harris, Bethan Shaw

Report No: [AHDB Use only]

This is the final report of a PhD project that ran from September 2020 to March 2025. The work was funded by AHDB, BBSRC, and the CTP FCR.

While the Agriculture and Horticulture Development Board seeks to ensure that the information contained within this document is accurate at the time of printing, no warranty is given in respect thereof and, to the maximum extent permitted by law, the Agriculture and Horticulture Development Board accepts no liability for loss, damage or injury howsoever caused (including that caused by negligence) or suffered directly or indirectly in relation to information and opinions contained in or omitted from this document.

Reference herein to trade names and proprietary products without stating that they are protected does not imply that they may be regarded as unprotected and thus free for general use. No endorsement of named products is intended, nor is any criticism implied of other alternative, but unnamed, products.

A series of approximately 10-12 thin, light blue wavy lines that sweep across the bottom of the page from left to right, creating a decorative footer element.

CONTENTS

1. INDUSTRY SUMMARY	4
2. INTRODUCTION	5
2.1. General	5
2.2. Woolly apple aphid	5
2.3. Earwigs	7
2.4. Woolly apple aphid and earwigs	9
2.5. Radio frequency identification	11
3. MATERIALS AND METHODS	13
3.1. The presence of earwigs and <i>Eriosoma lanigerum</i> in orchards in Kent.....	13
3.1.1. 2023 Experimental design	13
3.1.2. Apple growth stage	16
3.1.3. Earwig counts	16
3.1.4. Woolly apple aphid assessments	16
3.1.5. Other aphid assessments	17
3.1.6. Tree bed ground cover	17
3.1.7. Earwig molecular collections.....	17
3.1.8. Soil type.....	20
3.1.9. Statistical analysis	20
3.2. Impact of artificial shelters on the numbers of earwigs and <i>Eriosoma lanigerum</i> in an experimental apple orchard	21
3.2.1. Experimental design	21
3.2.2. Woolly apple aphid assessment.....	23
3.2.3. Earwig assessment.....	23
3.2.4. Statistics	24
3.3. Radio frequency identification mesocosm designs for the study of earwig behaviour	25

3.3.1.	Glue testing	25
3.3.2.	Glue testing statistical analyses	28
4.	RESULTS	29
4.1.	The presence of earwigs and <i>Eriosoma lanigerum</i> in orchards in Kent.....	29
4.2.	Impact of artificial shelters on the numbers of earwigs and <i>Eriosoma lanigerum</i> in an experimental apple orchard	39
4.2.1.	Earwig assessment.....	39
4.2.2.	Woolly apple aphid assessment.....	41
4.3.	Radio frequency identification mesocosm designs for the study of earwig behaviour	43
4.3.1.	Mortality	43
4.3.2.	Tag retention	44
5.	DISCUSSION	46
5.1.	Earwigs and <i>Eriosoma lanigerum</i>	46
5.2.	Earwig association with orchard and tree factors	49
5.3.	Radio frequency identification	53
5.4.	Grower recommendations	55
5.5.	Conclusions.....	55
6.	REFERENCES	57

1. Industry Summary

The background to this project was:

- *Woolly Apple Aphid* (*Eriosoma lanigerum*, WAA), is an important pest of apple trees
- The Common European earwig (*Forficula auricularia*) is a predator of WAA but adequate control is unreliable because earwig distribution and abundance is irregular
- *Forficula auricularia* ecology is understudied and a method of remotely tracking this species would be extremely useful
- Radio frequency identification (RFID) has not been used to track earwigs before

The key objectives of this project were to:

- Investigate the presence and abundance of earwigs and WAA in commercial apple orchards and identify orchard characteristics associated with either species. Surveying and molecular gut content analysis were used to investigate the importance of earwig predation of WAA
- Assess the impact of providing artificial shelters for earwigs, on the abundance of both earwigs and WAA in apple trees
- Test commonly used glues for their adhesion and toxicity when attaching tags to earwigs, to aid future research on behaviour. This included designing an RFID-enabled arena for collecting behavioural data from earwigs

The key findings from this project were:

- There is new evidence that earwigs contribute to the control of WAA in orchards
- The degree of WAA suppression by earwigs was weaker in organic orchards in the years studied
- Presence of earwigs was associated with bare earth in the tree row bed, but not with several food sources or orchard management type
- Earwig abundance may be limited by the availability of shelter in apple orchards
- RFID tracking may be used in laboratory arenas to study the behaviour of earwigs, but further improvements to the methodology are required
- Superglues (cyanoacrylate based glues) are toxic to earwigs and need to be avoided in future RFID studies; thermoplastic glues are preferable

The key takeaways for apple growers from this project are:

- Provide artificial shelters in the canopy of apple trees for earwigs
- Ensure there is bare ground in the row beds of apple orchards for earwigs to nest
- Avoid mechanical weeding within the tree row from November to May if possible (this will also help protect ground nesting bees)
- Try to avoid applications of insecticides known to be harmful to earwigs, particularly from May to October. Harmful insecticides include spinosad, indoxacarb, and deltamethrin
- Spirotetramat is not harmful to earwigs, and its effectiveness against WAA may be enhanced by the presence of earwigs
- *Aphelinus mali* (a parasitoid wasp that attacks WAA) and earwigs are compatible, and both are desirable for WAA control
- If augmentative releases of earwigs are attempted, ensure these are carried out over multiple years alongside management practices that protect them
- Do not use sticky banding around apple tree trunks to control WAA as this impedes earwigs reaching the canopy of the tree

- If a WAA infestation has become well developed during a growing season, earwigs will not be sufficient for control the pest within the season but may help prevent resurgence in future years
- Alternative sources of food, such as wildflowers, may not benefit earwigs specifically, but may be advantageous for other beneficials
- The fact that WAA does not appear to be a serious pest problem in an orchard may indicate that earwigs are preventing colonisation
- Earwigs also help to control many other pests, particularly other aphid species and codling moth
- Monitoring and recording numbers of natural enemies in trees alongside pest monitoring is recommended

The following report is an abridged version of the PhD thesis.

2. Introduction

2.1. General

Malus domestica (Bork; apple) is the second most abundant fruit crop in the world behind banana (O'Rourke, 2021; Vasylieva & Harvey, 2021; tonnes produced). In terms of revenue, however, apple far outstrips banana, with a global gross production value in 2016 of 38 million USA dollars (O'Rourke, 2021). Apples are grown in 96 countries, with China, the USA, Poland, Turkey, and Iran being the largest growers (Vasylieva & Harvey, 2021). One important pest of apple is the woolly apple aphid (*Eriosoma lanigerum*, Hausmann; WAA). Woolly apple aphid is widely regarded as increasing in severity over the last 20 years and can cause an estimated yield loss of 5% in apples (Brown *et al.*, 1995; Beers, Cockfield & Fazio, 2007; Beliën *et al.*, 2010; Dedryver, Le Ralec & Fabre, 2010; Bangels *et al.*, 2021). Currently, control of WAA in the UK relies on a small number of chemical insecticides, with only spirotetramat reported as being consistently effective (Ridley *et al.*, 2024; Cross *et al.*, no date). This makes current UK control of WAA susceptible to changes in pesticide regulation or the development of resistance by the pest to this single active ingredient. Therefore, there is a need to investigate alternative methods of WAA control. The common European earwig, *Forficula auricularia* (L.), is a predator of WAA, however, whether this species of predator can effectively control this pest in apple orchards is uncertain (Carroll, Walker & Hoyt, 1985; Nicholas, Spooner-Hart & Vickers, 2005; Quarrell, Corkrey & Allen, 2017; Happe *et al.*, 2018; Marshall & Beers, 2022; Alins *et al.*, 2023).

2.2. Woolly apple aphid

Woolly apple aphids inject saliva into apple trees when feeding. As many as 390 candidate effector molecules have been identified from the transcriptome of WAA salivary glands, which may be important in inducing galling - the main mechanism of WAA damage to apple (Wemmer, 2019).

Importantly, WAA is not known to act as a vector for any plant viruses (Blackman & Eastop, 1984; Barbagallo *et al.*, 1997). Gallling is a form of induced cell proliferation within the host plant and is not unique to WAA (Wool, 2004). Gall formation is induced by the feeding insect and is adaptive rather than coincidental. This is highlighted by the fact that certain aphid species produce consistent and highly structured gall shapes, in many cases providing shelters for the insect responsible (Pike *et al.*, 2002; Wool, 2004). Galls can also induce concentrated clusters of vascular tissue, which provide a greater volume of phloem and alter the structure of tissue to make sieve elements easier to access (Wool *et al.*, 1999). In the case of WAA, galls consist mainly of parenchyma, a relatively unstructured tissue, although they also induce the production of small pockets of vascular tissue (Nogueira *et al.*, 2024). Changes in the structure of cell walls in the parenchyma and phloem cells within the galls, as well as directly above and below them, help to restrict the flow of photoassimilates and water away from the gall, instead concentrating them near the feeding WAA colony (Nogueira *et al.*, 2024, 2025). This means galls directly disrupt the flow of nutrients within apple trees, while aphid feeding simultaneously removes nutrients, leading to reductions in growth and yield (Brown *et al.*, 1995; Dedryver, Le Ralec & Fabre, 2010; Nogueira *et al.*, 2025).

Woolly apple aphid induced gallling can occur without causing any obvious signs (from the exterior) within apple tissue, but frequently galls become large enough that they cause splitting of the bark and exterior wounds in the tree (Weber & Brown, 1988; Godfrey, 2024). These can then act as sites for pathogenic infection. In particular, galls may allow apple canker (*Neonectria ditissima*, Samuels and Rossman) to infect a tree (Asante, Danthanarayana & Cairns, 1993; Biello *et al.*, 2021; Childs, 1929). Honeydew excreted by WAA can also encourage the growth of sooty moulds (Ascomycete spp.), which in turn reduce the photosynthetic capacity of the tree (Shaw & Walker, 1996; Guerrieri & Digilio, 2008; Dedryver, Le Ralec & Fabre, 2010).

Woolly apple aphid is widely reported as increasing in severity over the last few decades, with many researchers attributing this to the decreased use of organophosphate insecticides, which are highly effective against WAA (Beers, Cockfield & Fazio, 2007; Beliën *et al.*, 2010; Dedryver, Le Ralec & Fabre, 2010; Bangels *et al.*, 2021). The apple best practice guide for the UK (Cross *et al.*, no date) states that in recent years, flonicamid, a previously effective aphicide, has reportedly had reduced effectiveness against WAA, perhaps as a result of reduced sensitivity of this species. Spirotetramat is recommended as the only remaining registered insecticide that provides effective control. Spirotetramat is a keto-enol insecticide which inhibits lipid biosynthesis, and is thus particularly effective against nymphal WAA because it prevents growth (Nauen *et al.*, 2007; Schoevaerts *et al.*, 2011). The compound is two-way systemic, meaning it is absorbed by apple trees and transported in both the xylem and phloem (and thus upwards and downwards;

Schoevaerts *et al.*, 2011; Goossens *et al.*, 2011). Importantly, spirotetramat targets edaphic WAA as well as aerial colonies, as WAA feeding anywhere on the tree will ingest the compound. In terms of area treated, spirotetramat was the third most-used insecticide in apple orchards in the UK in 2022 (Ridley *et al.*, 2024). There is also an EAMU (Extension of Authorisation for Minor Use) for spirotetramat on outdoor apple in Great Britain against WAA (EAMU Number: 1261 of 2022).

2.3. Earwigs

Due to the difficulty in studying earwig foraging in situ, much of the information on their diet comes from laboratory-based feeding experiments or gut content analysis. Earwigs are highly polyphagous and omnivorous. Common foodstuffs in orchards include pollen, leaves of various plants, algae, moss, lichen, and other insects (Beall, 1932; Crumb, Bonn & Eide, 1941; Lamb & Wellington, 1975; Phillips, 1981; Orpet, *et al.*, 2019a). Besides WAA (discussed below), earwigs are known to consume rosy apple aphid (*Dysaphis plantaginea*, Passerini; Dib *et al.*, 2016a; Dib *et al.*, 2016b; Dib *et al.*, 2020), apple aphid (*Aphis pomi*, Degreeer; Carroll, Walker & Hoyt, 1985), melon and cotton aphid (*Aphis gossypii*, Glover; Piñol *et al.*, 2009), codling moth larva (*Cydia pomonella*, Linnaeus; Boreau de Roincé *et al.*, 2012), brown marmorated stink bug eggs (though not efficiently, *Halyomorpha halys*, Stål; Bulgarini *et al.*, 2020), apple leaf curling midge (*Dasineura mali*, Keiffer; He, Wang & Xu, 2008), and diapsid scale insects (*Hemiberlesia lataniae*, Signoret; *H. rapax*, Comstock; *Aspidiotus nerii*, Bouche'; Logan, Maher & Rowe, 2017). The gut content analysis of Crumb, Bonn, and Eide (1941) and Phillips (1981) probably provide the best information on the proportions of different foods that earwigs feed on in the field, although it can be presumed that this will be highly variable between locations based simply on availability (Crumb, Bonn & Eide, 1941). In general, studies agree that more vegetable matter than animal is consumed, and that a variety of foods is preferred over single sources. Despite the social behaviour displayed during sheltering, intraspecific aggression has been reported during foraging (Lamb, 1975). Feeding hierarchies are established, with more dominant individuals feeding for longer. The hierarchy is not rigid, although the same individuals tend to rank highly on successive nights. Individuals with a higher body mass tend to rank more highly, although it is unclear if higher weight causes dominance, or dominance allows individuals to put on weight. It must be noted these observations were made on populations of earwigs contained in the laboratory, so may not be applicable to field conditions.

Due to their nocturnality, researchers frequently make use of refuge trapping as a method to study the abundance of earwigs, or simply to collect them. Refuge trapping involves providing an animal with an artificial shelter, which acts as both the trap structure and 'attractant'. Refuge traps for catching earwigs are often constructed from corrugated cardboard, although any structure which

provides lots of dark, tight spaces can be used. Studies have shown refuge traps placed on the trunks of trees tend to have the highest capture (Phillips, 1981; Hanel *et al.*, 2025). There is some evidence to suggest the availability of shelter in apple orchards is a population-limiting factor for earwigs (Moerkens *et al.*, 2009; Jana *et al.*, 2021). Studies have suggested this is not the case in kiwifruit vines (*Actinidia deliciosa*, Chev) but is the case in a mixed gravel-grassland environment (Lamb, 1975; Logan *et al.*, 2007). Predation by birds may be an important cause of mortality in unsheltered earwigs (Lamb, 1975; Gobin *et al.*, 2006). Currently, the navigational ability of earwigs is considered very poor, with individuals being incapable of relocating a previously used shelter if they travel more than approximately 50 cm from it (Lamb, 1975). However, the ability of earwig mothers to forage and return to their brood chamber to provision for their offspring suggests that it is possible for earwigs to re-locate sites. Also, when released into apple and pear orchards, earwigs showed very low levels of dispersal (Moerkens *et al.*, 2010). Ninety five percent of earwigs from species A moved less than 30 m in a month, for species B (which is more common in the UK; Phillips, 1981; González Miguéns *et al.*, 2020) 95% moved less than 8 m. Therefore, it may be that earwigs frequently return to the same shelter simply because they never move far from it (Phillips, 1981; Moerkens *et al.*, 2009).

Due to their omnivorous diet, earwigs can be a pest in many contexts. In cherries, strawberries, raspberries, grains, potatoes, cauliflower, cabbages, and gardens, they can cause economically important damage, which may outweigh any benefit they have in the consumption of other pest species (Crumb, Bonn & Eide, 1941; Orpet, Crowder & Jones, 2019b; Orpet, *et al.*, 2019a; Binns *et al.*, 2021; Binns, Macfadyen & Umina, 2022; Hanel *et al.*, 2023). As a result, control measures for earwigs have been researched (Crumb, Bonn & Eide, 1941; Maczey *et al.*, 2016). In other crops, namely apples, pears, citrus fruit, and kiwifruit, earwigs are thought to act mainly as a beneficial (Solomon, 1992; Evans & Longépé, 1996; Gobin *et al.*, 2006; Piñol *et al.*, 2009; Romeu-Dalmau, Piñol & Espadaler, 2012; Romeu-Dalmau, Espadaler & Piñol, 2012; Jana *et al.*, 2021). This is because the thicker skins of these fruit protect them from direct damage by earwigs, and while some secondary damage to fruit or to the trees may occur, this is outweighed by their consumption of more serious pests. As earwigs are considered both a predator and a pest, multiple researchers have investigated the possibility of removing earwigs from crops where they cause damage and releasing them into pome fruit orchards where they may control pest species (Evans & Longépé, 1996; Hanel *et al.*, 2023).

Spinosad, indoxacarb, chlorpyrifos, deltamethrin, azinphos-methyl, cypermethrin, diazinon, kaolin particles, thiacloprid, carbaryl, and flonicamid have all been shown to induce significant mortality in adult earwigs, while primicarb, gamma-hexachlorocyclohexane, fenitrothion, dimethoate, dichloro-diphenyl-trichloroethane (DDT), abamectin, chlorantraniliprole, fenoxycarb, acetamiprid, *Bacillus*

thuringiensis, pyriproxyfen, parathion-methyl, alpha-cypermethrin, fenthion, tebufenpyrad, vamidothion, propargite, tebufenozide, methoxyfenozide, spirotetramat, and emamectin benzoate are less harmful to adult earwigs (Ffrench-Constant & Vickerman, 1985; Cisneros *et al.*, 2002; Nicholas & Thwaite, 2003; Maher, Logan & Connolly, 2006; Markó *et al.*, 2008; Peusens & Gobin, 2008; Peusens, Belien & Gobin, 2010; Shaw & Wallis, 2010; Vogt, Just & Grutzmacher, 2010; Fountain & Harris, 2015; Malagnoux, Capowiez & Rault, 2015; Holý & Stará, 2020; Meunier *et al.*, 2020; Merleau *et al.*, 2022). However, Fountain & Harris (2015) showed that insecticides which do not kill adult earwigs may significantly slow the growth of immature earwigs. Males often show a higher susceptibility to insecticides than females (Malagnoux, Capowiez & Rault, 2015; Jana *et al.*, 2021).

The effect of organic, Integrated Pest Management (IPM), and conventional management of orchards on earwigs is somewhat unclear from the published literature. The results of Helsen *et al.* (2007), Logan, Maher, and Connolly, (2011), Malagnoux *et al.* (2015), and Simon *et al.* (2024) suggest that earwigs tend to be more abundant under organic management with fewer insecticide sprays. In contrast, Nicholas, Spooner-Hart and Vickers (2005), Quarrell, Corkrey and Allen (2017), and Happe *et al.* (2018) found similar numbers of earwigs in organic and IPM orchards. Transgenerational studies on unexposed offspring with parents from different management types show that earwigs experience some intergenerational effects from insecticide use, but in general earwig generations seem to recover well if insecticide sprays are stopped (Le Navenant *et al.*, 2021). There is evidence that earwigs can adapt to the use of insecticides either through behavioural changes or chemical resistance (Le Navenant *et al.*, 2019, 2021; Jana *et al.*, 2021). Soil tillage can reduce earwig abundance in vineyards, but other studies have failed to find a clear effect (Sharley, Hoffmann & Thomson, 2008; Moerkens *et al.*, 2012). One study discovered that earwigs appear to overwinter outside of orchards altogether (Romeu-Dalmau, Espadaler & Piñol, 2016).

2.4. Woolly apple aphid and earwigs

The containment studies that involved confining WAA and earwigs to small areas provide some of the most straightforward and unambiguous evidence for earwig consumption and control of WAA. Carroll, Walker and Hoyt (1985) are notable for finding a lack of WAA control when earwigs were confined to rootstocks with them. This may have been due to testing the effect of earwigs on already established WAA colonies, which is not the ideal situation for control. Edaphic colonies of WAA were deliberately introduced to the rootstocks in the study, meaning there would have been a consistent reservoir of WAA underground, which earwigs were unable to predate. Additionally, the rootstocks contained alternative aphid prey and presumably vegetable food sources as well. It has

been pointed out before that in-laboratory studies such as Asante (1995), earwigs may be overvalued as a control agent of WAA due to the lack of alternative food (Orpet, *et al.*, 2019a). Bischoff *et al.*'s (2024) experiment elegantly highlights the utility of having larger populations of earwigs when it comes to biocontrol. While methods can be imagined for enhancing the efficiency of a given number of earwigs, such as providing shelter close to WAA colonies, or removing alternative sources of food, simply increasing the number of earwigs seems more practical.

Unlike some of the other study designs discussed, all exclusion experiments studying earwig predation of WAA have had positive results in terms of biocontrol. Evidence based on exclusion can suffer from a lack of specificity, in that sticky bands, the typical exclusion method employed, will prevent all crawling insects from entering an apple tree canopy, not just earwigs. This is highlighted by the fact that Orpet, *et al.* (2019b) unintentionally excluded earwigs whilst trying to exclude WAA crawlers. However, Mueller, Blommers and Mols (1988) monitored other generalist predators in their exclusion experiments and found no significant difference in their abundance between treatments. They also claimed to have distinguished between evidence of earwig predation on WAA and that of other species, and are thus confident that earwigs were more important than any other natural enemy in their study. This ability has not been reported in other studies. Stap *et al.* (1987) similarly compensated for the lack of specificity of sticky banding in one of their experiments by applying sticky bands to all trees, but then releasing earwigs into some of the banded canopies, thus demonstrating unambiguously that earwigs were the species responsible for the observed decline in WAA abundance. The work of Gontijo, Beers and Snyder (2015) is of particular importance; while many researchers have focused on the question of which WAA natural enemy is the most important, their study highlights that focusing solely on a single species of natural enemy is unlikely to be the most effective solution for biocontrol of WAA. It is worth noting that several of these studies also used correlational evidence for the importance of earwigs in controlling WAA, and are therefore relevant to the section below (Stap *et al.*, 1987; Mueller, Blommers & Mols, 1988; Nicholas, Spooner-Hart & Vickers, 2005).

Overall, most correlational studies show that earwig abundance is negatively correlated with WAA abundance, with threshold values of earwig abundance identified by Nicholas, Spooner-Hart and Vickers (2005) and Quarrell, Corkrey and Allen (2017). It is worth noting that of these studies, four involved augmentative releases of earwigs (Mueller, Blommers & Mols, 1988; Orpet *et al.*, 2019a; Alins *et al.*, 2023; Hanel *et al.*, 2023), while five were conducted on experimentally unaltered populations of earwigs (Nicholas, Spooner-Hart & Vickers, 2005; Helsen *et al.*, 2007; Quarrell, Corkrey & Allen, 2017; Happe *et al.*, 2018; Marshall & Beers, 2021, 2022). Although, Quarrell, Corkrey and Allen (2017) deliberately selected orchards with a range of earwig abundances (note that Marshall and Beers, 2021, 2022 are considered the same experiment, and that while these are

referred to here as 'experimentally unaltered' populations of earwigs, the use of refuge trapping to monitor these populations may have altered the population dynamics of earwigs, rather, 'experimentally unaltered' means there was no attempt to deliberately change the number of earwigs between different treatments). Studies which used augmentative releases of earwigs may be less applicable to the conditions in a standard commercially managed orchard. Of the studies which did not find significant negative correlations between earwigs and WAA abundance, Happe *et al.* (2018) provided no discussion of this result. The mean number of earwigs per tree varied from 3 to 27.1, so there were occasions where earwigs should have been abundant enough to meet the thresholds for control outlined by Nicholas, Spooner-Hart and Vickers (2005) and Quarrell, Corkrey and Allen (2017). Therefore, this result does not have a clear explanation. In the experiment run by Marshall and Beers (2021, 2022), the high levels of WAA infestation were unexpected by the authors, as both earwigs and *A. mali* were present. As mentioned above, they attribute this to the exclusion of other aphid predators, particularly *Heringia* spp. of syrphid flies. *Heringia* spp. would not have been excluded in sticky band experiments, so this does not discount the effectiveness of earwigs, but does highlight the importance of full natural enemy complexes as in other studies (Gontijo, Beers & Snyder, 2015; Bergh & Stallings, 2016). The more recent studies by Alins *et al.* (2023) and Hanel *et al.* (2023) demonstrate how releases of earwigs take effect over multiple years. This is important, as it suggests early season abundance of earwigs is important, simply increasing earwig numbers after WAA is established is not enough to produce control. Note that Orpet *et al.* (2019a) also used molecular gut content analysis to assess earwig predation of WAA, and is therefore relevant to section below.

Orpet *et al.* (2019a) and Orpet, Crowder and Jones, 2019a, through molecular gut content analysis and video monitoring, provide some of the most direct evidence of earwig predation and efficacy in the field. In particular, the presence of WAA DNA in earwig guts at low WAA abundances highlights the strength of earwigs as a predator of WAA in nascent stages of colony development, rather than as a species capable of consuming every individual in large, well-established populations.

2.5. Radio frequency identification

Given the difficulty in observing earwigs during their active phase, a remote monitoring solution that can be applied to this species is desirable. One potential monitoring system is Radio Frequency Identification (RFID), a technology used in ecology to study the movement of individual animals. Unlike similar technologies, such as harmonic radar or LIDAR (Light Detection and Ranging), RFID allows the identification of each individual animal (Landt, 2005; Ngai *et al.*, 2008). From an experimental design standpoint, the RFID tag and RFID antenna/reader are the important components of an RFID system.

To the author's knowledge, no studies have been published using RFID on earwigs. Because of the difficulty in observing earwigs during the active portion of their daily routine, a remote monitoring solution to study the foraging or shelter use of earwigs is highly desirable. A 30 mg passive RFID tag suitable for use with a mobile antenna (such as that used by Pope *et al.*, 2015) would be approximately 50% of the mass of an average adult (own data), while active tags weigh even more. The smaller passive RFID tags for use with fixed antennas therefore seem like the most suitable for use with earwigs in terms of size and weight. However, the use of fixed antennas comes with challenges in experimental design. Due to their highly polyphagous nature, likely feeding locations seem impossible to determine in the field. The ready use of artificial shelters (such as those used for refuge trapping) may provide an opportunity to monitor earwigs in a manner similar to studies conducted on honeybees, with an antenna or directional reader placed at the entrance/exit of an artificial shelter. This would be an interesting opportunity to extend this type of experimental design to a sub-social species, as to the author's knowledge all such experiments thus far have been conducted in eusocial species. Alternatively, RFID-enabled mesocosms would allow the study of captive earwigs within an environment designed to answer specific research questions. A mesocosm-based study also has the advantage of dramatically reducing the number of tagged individuals that would be needed to generate robust datasets. An alternative to RFID for the study of earwigs within a mesocosm environment would be video monitoring. Because earwigs are nocturnal, cameras would need to operate in red light or infrared in order to observe earwigs while active. In addition, to enable software tracking of individuals, visual tags may be required unless shelters opaque to visible light can be provided which are transparent to the wavelengths detected by the camera (e.g. infrared). Monitoring with passive RFID tags may therefore represent a simpler solution to monitoring earwigs during darkness. Harmonic radar and LIDAR are both techniques for studying flying insects, and thus not particularly relevant to the study of earwigs.

Overall, there seem to be three main factors crucial to the success of natural control of WAA by earwigs. First, and perhaps most important, earwigs must be present in abundance. Not all earwigs present will feed on WAA, but larger populations of earwigs will lead to more complete searching of the environment and may help overcome any reduction in efficiency from alternative food sources. Second, earwigs must be present early in the season. Given the rapid rate of WAA reproduction, eating aphids before they can reproduce is far more efficient than attacking WAA at peak abundances. Thirdly, a full complement of other natural enemies ensures that WAA which escape predation by earwigs can be attacked by species with alternative evolutionary strategies. There is a particular complementarity with rapidly reproducing WAA specialists, which will be much more effective against WAA if large populations do become established in a season.

Given these findings from previous research, the key barrier to achieving consistent natural control of WAA appears to be the variable and unpredictable nature of earwig populations, in terms of both distribution and abundance. Due to their nocturnality, earwigs are difficult to observe while active in orchards, and instead a great deal of research has relied on refuge trapping. Earwig foraging behaviour, landscape-scale dispersal, and causes of mortality, are all poorly understood. In particular, there are still only speculative explanations for the population crash when moulting to adulthood. Discovering why earwigs are distributed so variably might allow growers to manage orchards to help produce a more consistent benefit from earwig predation of WAA.

Remote monitoring using RFID has the potential to provide valuable information on earwig behaviour, and answer some of the questions outlined above. Before being blindly adopted, however, care must be taken to develop a methodology for tagging which does not directly harm earwigs. This should be followed by attempts to quantify the effects of tagging on earwigs, to ensure that conclusions from tagging studies can be properly contextualised in comparison to 'natural' behaviour.

3. Materials and methods

3.1. The presence of earwigs and *Eriosoma lanigerum* in orchards in Kent

3.1.1. 2023 Experimental design

Twenty orchards were surveyed in 2023; seven of these were orchards used in 2022, while 13 were new orchards which had not previously been surveyed. For the new orchards, trees were assigned x-y coordinates using row number as an x coordinate and a tree's position along that row as a y coordinate. However, unlike in 2022, for the new orchards, x-y coordinates were generated randomly in Microsoft Excel® (Microsoft 365 MSO, v. 2501 Build 16.0.18429.20132, 64-bit) to select new trees for inclusion (no preliminary surveys were carried out). For orchards previously used in 2022, the same 10 trees were used. This meant 200 trees were included in the surveys in total in 2023. Half of the orchards were organically managed, while half were conventionally managed. Originally, the aim was for each of these management types to be represented by five Gala orchards, and five Braeburn orchards. This was achieved for the conventional orchards but was not possible for the organic orchards. Instead, eight of these were Gala, one was Braeburn, and one was Spartan. The orchards belonged to nine different growers, with one organic Gala orchard being an experimental orchard owned and managed by Niab, East Malling, UK. A full list of the orchards and trees used for the 2023 surveys, along with their respective grower, variety, and management style, is in Table 3-1. Three rounds of surveys were completed, roughly corresponding to the months of July, August, and September. During each survey, all 200 trees were visited and the monthly field measurements outlined below were taken. After each survey, a

round of molecular collections was carried out, during which earwigs were collected for gut content analysis from a subset of orchards which were selected based on the results from the previous survey (method detailed below). Pitfall trapping was carried out in a subset of orchards after the final round of molecular collections, in October.

Table 3-1. A list of orchards surveyed in 2023. Soil types were taken from the Soilscales for England and Wales dataset developed by the National Soil Resources Institute at Cranfield University. FDAL = Freely draining slightly acid loamy soils. IDLC = Slightly acid loamy and clayey soils with impeded drainage. HGL = Loamy soils with naturally high groundwater. SWLC = Slowly permeable seasonally wet and slightly acid but base-rich loamy and clayey soils. BRL = Freely draining slightly acid but base-rich loamy soils.

Orchard	Grower	Management Style	Whole/ subset	Variety	Used Last Year?	Soil Type
1	1	Conventional	Whole	Gala	Y	FDAL
3	2	Conventional	Whole	Gala	Y	FDAL
4	3	Conventional	Subset	Gala	Y	IDLC
5	3	Conventional	Subset	Braeburn	N	IDLC
6	3	Conventional	Subset	Braeburn	N	IDLC
9	4	Conventional	Whole	Braeburn	N	FDAL
10	4	Conventional	Whole	Braeburn	N	FDAL
11	4	Conventional	Whole	Braeburn	N	FDAL
12	5	Conventional	Whole	Gala	Y	FDAL
13	5	Conventional	Whole	Gala	Y	FDAL
14	6	Organic	Subset	Gala	Y	FDAL
15	6	Organic	Subset	Braeburn	N	FDAL
16	6	Organic	Whole	Gala	Y	FDAL
18	7	Organic	Whole	Gala	N	HGL
19	7	Organic	Whole	Gala	N	HGL
20	8	Organic	Subset	Spartan	N	SWLC
21	9	Organic	Whole	Gala	N	IDLC
22	9	Organic	Whole	Gala	N	IDLC
23	9	Organic	Whole	Gala	N	IDLC
24	10	Organic	Subset	Gala	N	BRL

The order in which orchards were visited within each round of surveys was not random. Typically, two orchards were visited each day, with these pairs of orchards being surveyed on the same day as each other in each of the three rounds of surveys. These pairings were based on proximity, and the practicality of visiting all orchards in a timely manner. Similarly, within each orchard all 10 trees were surveyed in a systematic manner to minimise the time taken. The order each pair of orchards was visited during the first round of surveys was haphazard; however, after the first round of molecular collections, an effort was made to leave as much time as possible between an orchard being visited for molecular collection and subsequently being visited for surveying. This was done to give the earwig population more time to stabilise from disturbance after the removal of some

individuals and their replacement with others. A full account of the dates and times each orchard was visited for surveys and molecular collections can be found in Tables A-3 and A-4.

3.1.2. Apple growth stage

As well as the date, the Pome Fruit BBCH (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie) growth stage of the trees in each orchard was recorded (Meier *et al.*, 1994).

3.1.3. Earwig counts

Two Wignests™ (Russel IPM Ltd., Flintshire, UK) were placed into each of the 10 trees in each orchard, in May of 2023. Wignests are artificial shelters designed for earwigs. They consist of two interlocking wooden pieces (44 mm by 60 mm; interlocked depth = 14 mm) held together and attached to apple trees with a plastic hook. The two interlocking wooden pieces created three small channels (8 mm diameter) which earwigs then use as shelter during the day. These channels also contain a dry proprietary diet as an attractant. Wignest placement was subject to the arrangement of branches on the trees, but where possible Wignests were taped to the trunk of the tree, in the middle of the canopy, approximately 1.5 m from the ground, and in positions shaded from direct sunlight. The number of earwigs occupying the two Wignests was counted by emptying the Wignests onto a plastic tray and tapping the Wignests against the tray to detach any remaining earwigs. The time of sampling was also recorded. All earwigs were then released at the base of the tree and the Wignests repositioned on the tree.

3.1.4. Woolly apple aphid assessments

The percentage of WAA infestation on each tree was qualitatively assessed according to European and Mediterranean Plant Protection Organization (EPPO) guidelines and was similar to Nicholas, Spooner-Hart and Vickers, 2005 and Quarrell, Corkrey and Allen, 2017, by estimating the percentage of tree limbs infested with WAA. Only tree limbs containing living colonies were counted. Any tree limbs containing only mummified WAA were discounted from the estimate of percentage infestation. These were identified by visually inspecting for holes where *Aphelinus mali* (Haldeman) had emerged, and a lack of wool. If any living aphids were present (such as in a colony made up of some WAA mummies and some live aphids), then the limb was still considered infested.

If WAA colonies were only on the trunk or rootstock of the tree, this was considered a low-level infestation (because WAA tends to spread from the rootstock and trunk onto the branches over time, trees which only have infested trunks represent an early stage of WAA development).

Consequently, the percentage infestation score for any such trees was limited to between 1 and 5% depending on the extent and size of the colonies on the trunk/rootstock.

3.1.5. Other aphid assessments

Green apple aphid, RLCA, and RAA were monitored if present. This was done according to EPPO guidelines (EPPO Standard PP 1/258, 2007) by counting the number of infested shoots. No RLCA, and only two trees containing GAA, were detected in the survey. The presence of these two species was therefore not considered in modelling.

3.1.6. Tree bed ground cover

Square quadrats (50 cm x 50 cm) were placed at the base of each tree, perpendicular to the tree row and touching the trunk/post/rootstock/guard (if a guard was present). The percentage cover of bare ground, moss, herbaceous plants, and mulch was estimated by counting the number of squares in the grid filled with each type of ground cover.

3.1.7. Earwig molecular collections

The collection of earwigs for molecular gut content analysis was carried out in the weeks after the earwig and WAA counts (and other associated surveys). Ten orchards were selected for inclusion in this sampling each month by ranking the orchards by their most recent earwig count from the survey, and selecting every second orchard for inclusion (*e.g.* the orchard with the most earwigs, the orchard with the 3rd most earwigs, the orchard with the 5th most earwigs, *etc.*). The 10 orchards selected this way were visited early in the morning, and earwigs were collected for molecular gut content analysis. Five of the 10 trees surveyed before were randomly selected, and up to 10 earwigs from each of these five trees were taken from the Wignests for molecular gut content analysis. The first 10 earwigs to be shaken loose from the Wignests were taken; any extra earwigs loosened were released at the base of the tree. The earwigs taken for sampling were replaced by an equivalent number of earwigs released at the base of the tree, to minimize the effect on future surveys and molecular collections. Replacement earwigs were collected from Niab, East Malling, UK, from a variety of fruit crops by a mixture of refuge trapping, tap sampling, and collection by hand.

The earwigs taken for molecular gut content analysis from a given tree were placed in a clear plastic bag together, which was placed into a new plastic tube and stored in a box of ice, with the tree they were captured from and time at which they were put on ice recorded. They were then taken back to Niab, East Malling, UK, and stored at -80 °C. This killed and preserved these earwigs until they were dissected and processed using a Qiagen DNeasy blood and tissue kit to extract DNA from the gut contents.

Before starting dissections, all earwigs from a given tree were removed from the -80 °C freezer, by one minute submersion in 70% ethanol followed by one minute submersion in 5% bleach. The earwigs were then gently dried on a piece of blue roll. The dissections were carried out on a cut piece of blue roll, with a new piece of blue roll being used for each individual. Four sets of forceps were used in two sets of two, while one set was in use for dissection the other was left to sterilise in 5% bleach (approximately 5 mins). All forceps were dried on a piece of blue roll prior to the dissection of each individual. The dissection process used was modified from that used by Daniel Hausler (*pers. comm.*). First, on the ventral side, the posterior-most segment of the abdomen prior to the sternite which holds the cerci was removed. Then, both the dorsal and ventral anterior-most abdominal segments were separated from the thorax. The hindgut and foregut were also separated at this point. The head was then separated from the thorax and pronotum, and the foremost section of the digestive tract was separated from the base/posterior of the head (pulling the gut through the interior cavity of the pronotum often squeezes the contents of the gut out of the digestive tract). The thorax and pronotum were gently pulled in the posterior direction, leaving the foregut behind. The hindgut was extracted from either end of abdomen depending on how strong the attachment to the plate holding the cerci was. If this connection was strong, the cerci and attached plate could be used to pull the hindgut out of the abdomen from the posterior end. If it was weak, then the forceps could be used to grasp the hindgut directly and pull it from the anterior end of the abdomen. This dissection method was followed as possible, but was adapted ad-hoc as required to extract the entirety of the gut without losing the gut contents. Once extracted, both the hindgut and foregut from each individual earwig were placed into a 2 mL PCR-clean locking Eppendorf tube. At the end of the day, these were placed back into the -80 °C freezer, and stored until the extraction process was started.

The method for extraction was taken from the Qiagen supplementary protocol: Purification of total DNA from insects using the DNeasy® Blood & Tissue kit (Available at: <https://www.qiagen.com/us/products/discovery-and-translational-research/dna-rna-purification/dna-purification/genomic-dna/dneasy-blood-and-tissue-kit>). The following modifications were made to this. At the first step, two 4 mm diameter grade 100 hardened 52100 chrome steel ball bearings (Simply Bearings Ltd., Leigh, Lancashire, UK) were placed into a 2 mL locking Eppendorf tube, with the dissected earwig guts. These tubes were placed into a Geno/Grinder 2010 tissue homogenizer (SPEX SamplePrep, Metuchen, USA), in a metal block chilled to -80 °C, and the Geno/Grinder run at 1500 rpm for 1.5 mins. This was repeated three times for each set of samples. In between each run in the Geno/Grinder, any tubes in which the ball bearings had become lodged in the earwig guts were manually tapped against the bench surface until the ball bearings were loosened, before being placed back into the Geno/Grinder. After step 2 of the protocol, and the addition of the proteinase K in step 3, but before the incubation step, the ball bearings were

removed using a magnet. Care was taken not to contact the inside of the Eppendorf tubes with the surface of the magnet, and the magnet was cleaned with ethanol, and then dried on blue roll, after extracting the ball bearings from each sample. During the incubation step, either a water bath at 56 °C or a Stuart® SI500 orbital incubator (Cole-Parmer UK, Cambridgeshire, UK) set at 200 rpm and 56 °C was used. Most samples were left to incubate for a total of 3 hours, being removed from the water bath or orbital incubator every 30 mins to vortex, as in 2022. However, samples 61 to 180 were instead left overnight in the orbital incubator, and the rest of the DNA extraction protocol was carried out the following day. Due to the shaking of the orbital incubator being deemed insufficient to compensate for the lack of vortexing, this method was abandoned for samples 181 onwards. Steps 4 to 7 were carried out as outlined in the protocol. For steps 8 and 9, two 100 µl elution steps were used, rather than a single 200 µl elution step or two 200 µl elution steps as in the Qiagen protocol.

Once DNA was extracted, polymerase chain reaction (PCR) was run on each pooled sample using the following thermocycler settings: 95 °C for 3 mins, [95 °C for 30 s, 48 °C for 45 s, 72 °C for 45 s] for 40 cycles and 72 °C for 3 mins. The primers used were '35F' (5'-GGAA TAATTGGTTCATCCTTA-3') and '300R' (5'-CTACAAATTATTATTATTA AAGAAGGG-3') published by Orpet *et al.* (2019a). The reaction mix was made up of 4 µl undiluted DNA extraction elute, 1 µl of 5 µM of each primer (2 µl total), 6.5 µl of molecular grade water (hereafter 'water'), and 12.5 µl of PCRBIO Taq Mix Red (PCR Biosystems Ltd., London, UK). The PCR product was then run on a 1.5% agarose gel with GelRed® (Biotium Inc., Fremont, USA), and visualised using a Gel Doc™ XR+ with Image Lab™ software (Bio-Rad Laboratories Ltd., Watford, UK). The presence of bands at 265 bp, in line with the positive control bands, was taken as a positive result. Positive controls for the PCR were created by processing whole WAA with the same DNA extraction method (Godfrey, 2024). For each positive control sample, 10 to 20 WAA were used, and the extraction elute was diluted to 1:100 using water for use in the PCR. Experimental negative controls were created for the PCR by taking earwigs captured from strawberry tunnels at Niab, East Malling, UK, starving them for 48 hours, and then dissecting and processing them for DNA extraction using the same method as the field-collected earwigs. A PCR negative control was run using 4 µl of extra water in place of DNA.

The PCR products of three positive results were diluted to 1:10 with water and sent for Sanger Sequencing by Eurofins (Ebersberg, Germany). For each sample, the forward and reverse sequences were combined for each gene to create a consensus sequence using Geneious v. 2019.2.1 (Auckland, New Zealand), after being visually inspected and trimmed (L. Farwell, *pers. comm.*). The consensus sequences were then searched in NCBI BLAST® (National Library of Medicine, Bethesda, USA; Basic Local Alignment Search Tool), using the core nucleotide

database and megablast program. The closest matching genome was identified by the highest percentage identity with an e-value of < 0.0001 .

Due to the results of the BLAST search, a follow-up experiment was performed by testing the 35F and 300R primers on *Rhopalosiphum padi* (L.) which were provided from a culture kept at Harper Adams University (T. Pope, *pers. comm.*). Five samples, each consisting of four individual *R. padi* adults (20 aphids used in total), were processed for DNA extraction using the same method as the earwig guts, with the same thermocycler settings and PCR reagents as before. The DNA extraction was carried out on 2024.11.08 and the PCR on 2024.11.13.

3.1.8. Soil type

The soil type for each orchard's location was taken from the Soilscape for England and Wales interactive map provided by the UK Soil Observatory and developed by the National Soil Resources Institute at Cranfield University. This dataset classifies areas as 1 of 27 possible soil types (Soil Image © Cranfield University and for the Controller of HMSO, 2025 used with permission). Each orchard was located on the interactive map, and the soil type at that location recorded. This information was treated as a categorical variable (see below) with no consideration for the description of the soil type. For example, “freely draining slightly acid loamy soils” was treated as no more or less similar to “freely draining slightly acid but base-rich loamy soils” than “loamy soils with naturally high groundwater”.

3.1.9. Statistical analysis

Statistical analyses of the 2023 survey data were conducted in R studio (v. 2012.12.1) using R (v. 4.4.2) and the following packages: openxlsx (Schauberger & Walker, 2025), lme4 (Bates *et al.*, 2015), lmerTest (Kuznetsova, Brockhoff & Christensen, 2017), visreg (Breheny & Burchett, 2017), emmeans (Lenth, 2025), glmmTMB (Brooks *et al.*, 2017), car (Fox & Weisberg, 2019), ggfortify (Tang, Horikoshi & Li, 2016) and bindata (Leisch, Weingessel & Hornik, 2024). Generalised linear modelling was used to create mixed-effect models for WAA and earwigs. To provide a point of comparison for the importance of the factors measured in the study, a ‘baseline’ model was created for each species each year. To fit the baseline models, the experimental design structure was included as random intercepts, which consisted of tree within orchard within grower. Survey, as a fixed effect, was then included if significant. No other fixed effects were considered for the baseline models. Each baseline model was then compared to the relevant ‘assembled’ model using Akaike’s Information Criterion (AIC). The assembled models included tree as the only random intercept, to avoid pseudoreplication. All other factors were then considered as fixed effects, with fixed effects included or excluded from the model based on any improvement

(lowering) of the AIC and significance of the effect. For all random effects, random intercepts were used but not random slopes. This was due to random slopes requiring larger datasets.

Measurements were treated in the following ways for modelling. The grower, orchard, and tree were considered categorical. The number of the survey within a year (referred to simply as survey, and roughly corresponding to different months) was treated as categorical years. Whether an orchard was managed organically or conventionally (referred to as management style) was treated as categorical. The uncapped earwig counts from 2023, were converted to binary presence or absence variables due to the high number of zeros. The WAA estimated percentage infestations from 2023 were converted into binary presence or absence variables due to the high number of zeros. In 2023, GAA and RLCA were discarded, but RAA shoot count was converted to a binary presence or absence variable due to the high number of zeros. In 2023, the percentage ground cover of plants and bare earth was converted to a 'high'-low' binary variable, with low being given to any value < 50%, and high given to any value ≥ 50%. The percentage ground cover of moss and mulch were converted to a binary presence or absence variable, due to the high number of zeros for both measurements. In 2023, the soil type was treated as a categorical variable. In 2023, apple variety was tested in models using a subset of the data which excluded the single Spartan orchard, and was thus treated as a binary variable of Gala or Braeburn. Note that all modelling which did not include variety as a factor was completed on the full dataset, including the final models presented here.

The accepted models were:

- 2023 WAA Baseline had tree within orchard within grower as nested random effects with the month of survey as a fixed effect
- 2023 WAA Assembled had tree as a random effect; management style, month of survey, earwig presence, RAA presence, and moss presence as fixed effects; with interaction effects between management style and the month of survey, and management style and earwig presence
- 2023 Earwig Baseline had tree within orchard within grower as nested random effects and the month of survey as a fixed effect
- 2023 Earwig Assembled had tree as a random effect, the month of survey, RAA presence, and bare earth abundance as fixed effects

These are discussed further in section 4.1.

3.2. Impact of artificial shelters on the numbers of earwigs and *Eriosoma lanigerum* in an experimental apple orchard

3.2.1. Experimental design

An experimental apple orchard at Niab, East Malling, UK (coordinates: 51.286527, 0.465566) was used for the study. The orchard contained nine 12 x 12 (144 trees) blocks of fully-grown apple trees (planted in 2000), with Italian alder hedgerows separating the blocks. The study was limited

to a single variety of apple, Royal Gala, to avoid variability in susceptibility to WAA between varieties. Royal Gala trees were present in four of these blocks (Blocks 3, 5, 6, and 7) in each case consisting of three rows of 12 trees. Twenty-two Royal Gala trees from each block were selected for sampling (88 trees in total), by including the central 7, then 8, then 7, trees, from each set of 3 rows. This was done to limit edge effect on trees at the end of the rows, by excluding 2 or 3 trees from either end of each row.

All four blocks containing Royal Gala apple trees were treated with the same spray programme for the years 2015 to 2021, although no insecticides were applied during the years 2015, 2017, and 2018. The spray records for the years 2012, 2013, and 2014 were not available. Older records were available for the years 2007 to 2011, and during these years the blocks used in this study were treated differently. Table 3-2 gives the names, active ingredients, and frequencies of the insecticide sprays applied to the Royal Gala trees.

The trees in Block 7 had been provisioned with corrugated cardboard bands (10 cm wide and 40 cm long) around the trunks to collect codling moth larvae for another unrelated experiment (Mateos-Fierro, *pers. comm.*). Bands were tied around the trunk of the trees at 40 cm above the ground, fixed in place using electrical tape, and were in place for three months before the first WAA assessment took place.

Table 3-2. Active ingredients of insecticide sprays applied to the Niab, East Malling, UK, experimental orchard blocks including the number of applications. The estimated IOBC toxicity rating of each chemical is given for earwigs (*Forficula auricularia*) and woolly apple aphid (*Eriosoma lanigerum*; WAA). These data are from spray records for the years 2007 to 2011, and 2015 to 2021. Toxicity ratings are on a scale from 1 to 4, with 1 being the least harmful and 4 being the most harmful.

Active Ingredient	Block	Number of Sprays per Block				IOBC Toxicity Rating	
		3	5	6	7	Earwigs	WAA
pirimicarb		1	1	1	1	1	4
spirotetramat		1	1	1	1	1	4
thiacloprid		6	6	7	10	2	1
chlorantraniliprole		4	2	2	2	1	1
acetamiprid		1	1	1	1	2	3
pyriproxyfen		1	1	1	1	2	3
fenoxycarb		2	2	1	4	1	1
flonicamid		1	1	1	2	1	4
chlorpyrifos		5	5	8	7	4	4
methoxyfenozide		6	6	4	7	1	1
indoxacarb		5	4	4	4	3	1
Total		33	30	31	40		

3.2.2. Woolly apple aphid assessment

Woolly apple aphid colony counts were carried out on the labelled trees once each. Blocks 3 and 6 were surveyed on 2021.07.27, Block 5 on 2021.07.29, and Block 7 on 2021.08.01. Assessments were visual inspections of the trees from both sides of the row, looking for the distinctive white wax produced by the aphids. Each distinct mass of WAA was considered a separate colony, with no consideration of size. Initially colonies were divided into three categories, depending on if the colony appeared on the rootstock, trunk, or branches of the tree; however, these were combined into a total count from each tree for analysis due to most colonies occurring on the branches.

3.2.3. Earwig assessment

Earwig counts were carried out on the same trees used for the WAA colony counts. Blocks 3 and 6 were searched on 2021.08.13 and Blocks 5 and 7 were searched on 2021.08.15. On each night, two searches were performed per tree, one along each side of the row. Each search lasted one minute and thirty seconds, for a total of three minutes per tree, and was conducted using a handheld torch. Light was passed over the branches and foliage of the trees at various angles from

approximately 30 cm. Earwigs were categorised as male, female, or immature (no immature earwigs were recorded), based on the shape of the cerci. Adult male earwigs have strongly curved cerci, while female cerci are much straighter with only a slight curve at the tip. Immature earwigs have cerci which in shape resemble that of females, but their cerci are thinner and smaller in proportion to their bodies and their elytra are underdeveloped. All earwig searches were completed after sunset (earliest search started at 22:15, latest search started at 02:20).

3.2.4. Statistics

As the earwig count data were not normally distributed, they were analysed using a Wilcoxon test to test for an impact of artificial shelters. A Kruskal-Wallis test was conducted to compare the earwig counts between the different orchard blocks, excluding Block 7 which contained the artificial shelters.

The impact of artificial shelters (used by earwigs) on WAA colony counts was similarly analysed using a Wilcoxon test. The WAA colony counts of the different blocks were compared using Kruskal-Wallis tests, with tests conducted both including and excluding Block 7. Post-hoc analysis of these tests was carried out using Dunn tests with Bonferroni correction.

All analyses were conducted in R studio (v. 2012.12.1) using R (v. 4.2.2), and employing the openxlsx (Schauberger & Walker, 2025), lme4 (Bates *et al.*, 2015), lmerTest (Kuznetsova, Brockhoff & Christensen, 2017), lmerTest (Zeileis & Hothorn, 2002), FSA (Ogle *et al.*, 2025), and visreg (Breheny & Burchett, 2017) packages.

The cumulative toxicity rating for each orchard block was calculated using similar methods to Thomson & Hoffmann (2006), using ratings in accordance with the International Organisation for Biological and Integrated Control's (IOBC) toxicity ratings, but estimated using information from primary sources and/or product labels due the IOBC side effects database being unavailable (at time of writing; Table 3-3). These ratings correspond to the following scale: 1 = low toxicity (harmless, < 25 % mortality), 2 = slightly harmful (25–50 % mortality), 3 = moderately harmful (50–75 %), and 4 = very harmful (> 75 % mortality) (McKerchar *et al.*, 2020).

Table 3-3. The cumulative toxicity score for each orchard block used in this study, calculated using methods from Thomson & Hoffmann (2006), with IOBC toxicity ratings estimated for earwigs (*Forficula auricularia*) and woolly apple aphid (*Eriosoma lanigerum*; WAA) from available studies. The higher score represents a higher toxicity to the insects.

Block	Cumulative Toxicity Score	
	Earwigs	WAA
3	33	28
5	31	28
6	41	37
7	41	37

3.3. Radio frequency identification mesocosm designs for the study of earwig behaviour

Earwigs were collected from an experimental apple orchard at Niab, East Malling, UK (coordinates: 51.286527, 0.465566), on the 2024.08.26, using refuge trapping with Wignests® (Russell IPM Ltd., Flintshire, UK). The collected earwigs were kept at room temperature for up to 12 days prior to the experiment, in two Perspex boxes (210 x 105 mm at base, 227 x 120 mm at top, 85 mm vertical height, lid attached). The Wignests the earwigs were captured in were placed directly into these boxes. The Wignests contained an artificial diet as bait; this food source was supplemented with ground dried cat food (Nestle Purina UK Manufacturing Operations Ltd., York, England). Distilled water was provided once a day on weekdays.

3.3.1. Glue testing

Six glues were tested (Table 3-4), either with or without passive RFID tags, giving 12 experimental treatments and one control treatment. Ten earwigs (five males and five females) were haphazardly selected for inclusion. Where tags were applied, these were mic3® Q1.6 RFID tags (Microsensys GmbH, Erfurt, Germany). The tags weighed ≈ 2 mg and were $1.6 \times 1.6 \times 1.3$ mm in size. Three earwigs escaped during the experiment; data from them was discarded. Each earwig was placed individually in a tube and CO₂ applied to the tube using a lance until the earwigs became motionless. The earwigs were left in the CO₂-filled tube for an additional minute. After this, each earwig was weighed, placed in a bee marking cage (Serlium Bee Queen Bottle Marker, Guangdongsheng, China), and the treatment (glue) was applied to the centre of their elytra. Depending on the texture of the glue, each glue was either applied directly from the container to the elytra of the earwigs, or applied first to a piece of waxed paper, and then transferred to the

elytra of the earwigs using a cotton bud. For glue-with-tag treatments, tags were then pressed into the glue on the elytra using a set of forceps. Each earwig was left in the bee marking cage either until they recovered and began moving (this was usually first indicated by antennal movements), or until 20 minutes had elapsed. The bee marking cages had a grid with an aperture size of 4 mm, attached to a hollow plastic cylinder weighing 15.4 ± 0.1 g (\pm standard deviation). The platform the earwigs were placed on was covered in foam. The stem of the platform the earwigs were placed on extended beyond the end of this cylinder. To hold the earwigs in place, the end of this stem was placed in a tray of ice to hold the bee marking cage upright without the cylinder contacting the ice (Figure 3-1). This meant the weight of the cylinder was supported by the earwigs and surrounding platform. Ice was used as a substrate due to the flexibility it allowed in placement of the bee marking cages, but it was not expected to have a significant cooling effect on the earwigs.

Table 3-4. The six glues used in this experiment, their binding agents, and the addresses of the manufacturers.

Glue Name	Binding Agent (if different)	Manufacturer
Araldite	Epoxy	Huntsman Advanced Materials (Switzerland) GmbH, Klybeckstrasse 200, CH-4057 Basel
Thermoplastic Glue		Bostik Limited, Common Road, Stafford, England, ST16 3EH
Eyelash glue	Latex	Harlington Group Limited, C/O Apex Accountancy, Office Suite 134 First Floor, 4 Longwalk Road, Stockley Park, Uxbridge, England, UB11 1FE
Shellac		Libéron Limited, Mountfield Industrial Estate, Learoyd Road, New Romney, Kent, TN28 8XU
Gorilla glue	Cyanoacrylate	Gorilla Glue Europe Limited, 26 Eaton Avenue, Buckshaw Village, Chorley, England, PR7 7NA
Gorilla gel		Gorilla Glue Europe Limited, 26 Eaton Avenue, Buckshaw Village, Chorley, England, PR7 7NA

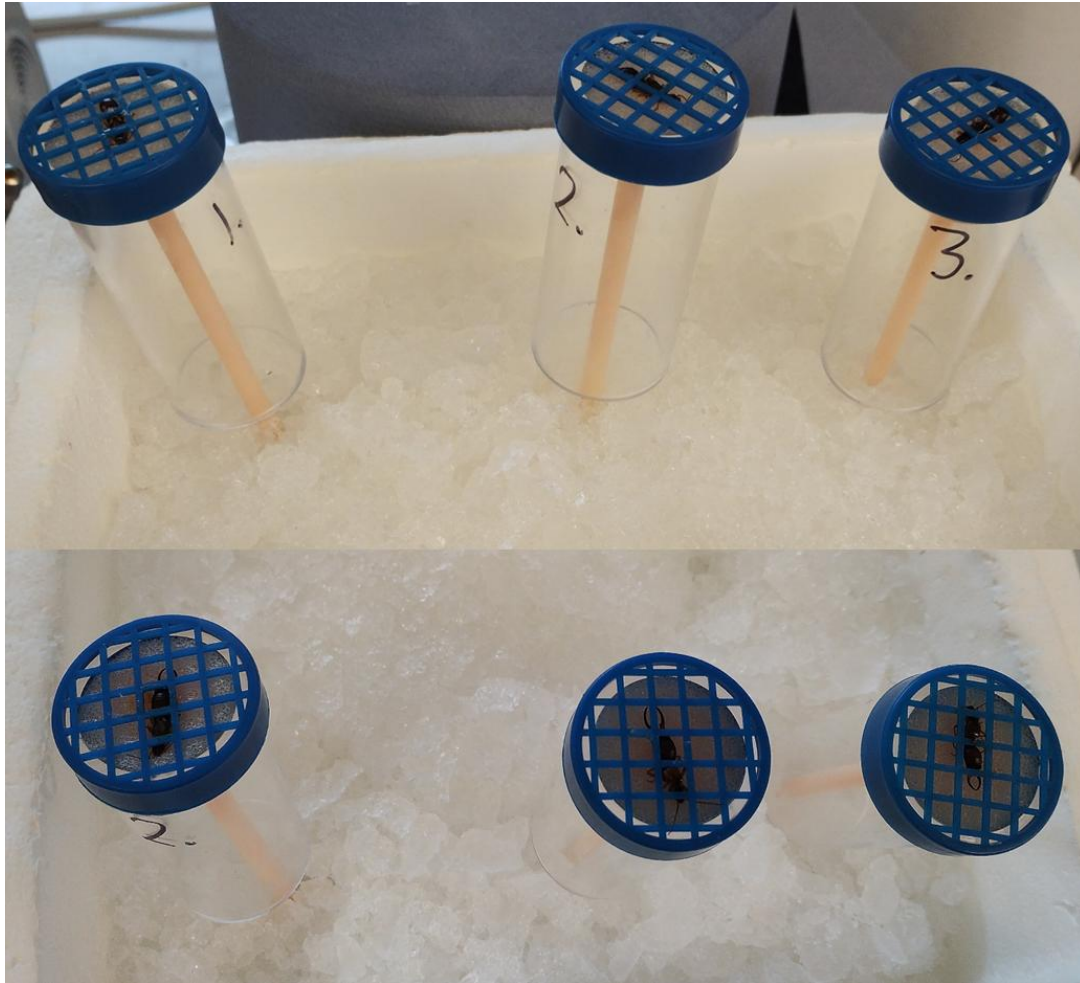


Figure 3-1. Two images showing anesthetised *Forficula auricularia* which have been placed into a bee marking cage for the application of glue (with or without a tag) onto their elytra. The bee marking cages were placed in ice to keep them upright while allowing the weight of the mesh and attached plastic cylinder to rest on the *F. auricularia*. Individuals remained in these cages for up to 20 minutes, or until they showed signs of recovery from anaesthetisation.

After 20 minutes or once active, earwigs were placed in individual Perspex containers (136 × 76 × 60 mm (length × width × height, lid attached)), with ventilation provided through holes covered in a fine mesh. Ground dried cat food (Nestle Purina UK Manufacturing Operations Ltd., York, England) was provided in sample tube lids. Distilled water was provided in plastic pipette bulbs sealed with a piece of sponge cloth (Specialist sponge cloths, Mapa Spontex UK Ltd., Staffordshire, England). On the second day of the experiment, earwigs were provided with one half of a prototype Wignest™ (Russell IPM Ltd., Flintshire, UK). This was to avoid providing earwigs with any heavy objects to scrape tags off against for the first night while slower setting glues might still not have dried fully. This behaviour was previously observed in pilot tests for this experiment (Video A-1). The first set of treatment was applied on 2024.08.28 and the last on 2024.09.06. Including the day of tag/glue application, the earwigs were observed for 14 days, or until they died, or the tag detached. Once an individual exited the experiment for one of these three reasons, it was

reweighed, and if necessary anaesthetised with CO₂, as before, to remove the tag. Starting at 17:00 each day (typically requiring 40 minutes), and 2 hours after treatment, each earwig was provoked to move by manual handling and categorised as either alive, moribund, or dead. An earwig was considered moribund if it showed antennal or leg movements but was incapable of co-ordinated locomotion. In addition, on every second day, earwigs were placed in a small sample tube (22 mm square base, 32 mm diameter rounded top, 54 mm height) within their container (approximately 5 mm clearance between top of tube and lid of container) and left overnight. The next morning, starting at 09:00 (typically taking 20 minutes) it was recorded if the earwig had escaped the sample tube by successfully climbing the vertical surface. Any earwig still within the sample tube were released before removing all the tubes. If during observations at the end of the day an individual displayed the ability to climb vertically on the sides of their box, this was instead recorded as an immediate success and that individual was not placed in the sample tube overnight.

3.3.2. Glue testing statistical analyses

To analyse the effects of treatment on mortality and tag retention, generalized linear models were fitted. For mortality (status as 'alive' or 'dead' by the end of the experiment) a binomial model was fitted, which had only treatment as a fixed effect. This model had an Akaike Information Criterion (AIC) of 58.327, which was better (lower) than the AIC of models of mortality including earwig sex, weight, or time spent in the bee marking cage as fixed effects. A Fisher test, and pairwise Fisher test, were completed to compare the mortality for each treatment, with the pairwise Fisher test using Bonferroni correction for multiple comparisons.

For tag retention (the number of days a tag remained attached), a negative binomial model was fitted, which included treatment, the time spent in the bee marking cage, and the interaction between these two factors, as fixed effects. This model had an AIC of 299.620, which was better than models of tag retention which included sex or weight as fixed effects. The model for tag retention was fitted to a subset of the data containing only data from the treatments which included tags, and only from earwigs which survived the experiment. A Kruskal-Wallis test, and pairwise Wilcoxon test, were conducted to compare the median days tagged for each treatment (using the same subset of data as the model), with the Wilcoxon test using Bonferroni correction for multiple comparisons. All analyses were conducted in R studio (v. 2024.12.0) using R (v. 4.4.2) and employing the openxlsx (Schauberger & Walker, 2025), car (Fox & Weisberg, 2019), dplyr (Wickham *et al.*, 2023), MASS (Venables & Ripley, 2011), ggplot2 (Wickham, 2009), rstatix (Kassambara, 2023), and onewaytests (Dag, Dolgun & Konar, 2018) packages.

4. Results

4.1. The presence of earwigs and *Eriosoma lanigerum* in orchards in Kent

The 2023 WAA Baseline model (Table 4-1) consisted of tree within orchard within grower as nested random intercepts, with survey as a fixed effect. This model had an AIC of 510.2, with orchard as the most powerful random effect. The 2023 WAA Assembled model (Table 4-2) had tree as the only random effect. Survey, management style, earwig presence, RAA presence, and moss presence were included as fixed effects, as well as interactions between earwig presence and management style, and survey and management style. This model had an AIC of 538.7. Variety, soil type, mulch presence, plant abundance, and bare earth abundance were all excluded from the model. There was the highest number of WAA-occupied trees in July, the fewest in August, and an intermediate number in September (Figure 4-1). Woolly apple aphid was less likely to be found on trees where moss cover was present in the row bed (Figure 4-2). Figures 4-3 and 4-4 show the individual effects of management style and earwig presence on WAA presence. More trees were occupied by WAA in organic orchards, and fewer trees were occupied by WAA when earwigs were present. However, Figure 4-5 shows the interaction between these two factors. When earwigs were absent, trees in conventionally managed orchards had a slightly lower probability of containing WAA than organic trees. But, when earwigs were present, the probability of finding WAA in a conventional tree was greatly reduced, while the probability of finding WAA in an organic tree was very similar regardless of the presence of earwigs. Figure 4-6 shows the interaction between management style and survey. While organic trees had a consistently higher probability of containing WAA than conventional trees in July and August, the number of trees occupied by WAA in conventional orchards continued to decline in September, but in organic orchards began to increase again. Trees had a higher probability of containing WAA if they contained RAA (Figure 4-7).

Table 4-1. A model for the presence or absence of WAA from 600 pseudo-trees ($n = 200$ trees, 3 surveys). AIC = Akaike Information Criterion. DF = Degrees of Freedom. Std. = Standard.

2023 WAA Baseline			
AIC	510.2		
Deviance	498.2		
DF residuals	594		
Random Effects			
Name	Type	Variance	Std. deviation
Tree	Intercept	0.4247	0.6517
Orchard	Intercept	3.2228	1.7952
Grower	Intercept	1.4746	1.2144
Fixed Effects			
Name	Estimate	Std. error	<i>p</i> value
Intercept	-1.2435	0.635	0.0502
Survey 2	-1.3448	0.3221	< 0.001
Survey 3	-0.5743	0.2906	< 0.05

Table 4-2. A model for the presence or absence of WAA from 600 pseudo-trees ($n = 200$ trees, 3 surveys). AIC = Akaike Information Criterion. DF = Degrees of Freedom. Std. = Standard.

2023 WAA Assembled			
AIC	538.7		
Deviance	516.7		
DF residuals	589		
Random Effects			
Name	Type	Variance	Std. deviation
Tree	Intercept	4.661	2.159
Fixed Effects			
Name	Estimate	Std. error	p value
Intercept	1.1347	0.7958	0.154
Organic	-2.2195	0.9105	< 0.05
Survey 2	-2.1412	0.6355	< 0.001
Survey 3	-2.9908	0.7247	< 0.001
<i>F. auricularia</i> present	-2.636	0.7185	< 0.001
RAA present	1.5821	0.5159	< 0.01
Moss present	-1.6337	0.5996	< 0.01
Organic * Survey 2	1.1574	0.7386	0.117
Organic * Survey 3	3.5279	0.8401	< 0.001
Organic * <i>F. auricularia</i> present	3.0682	0.8611	< 0.001

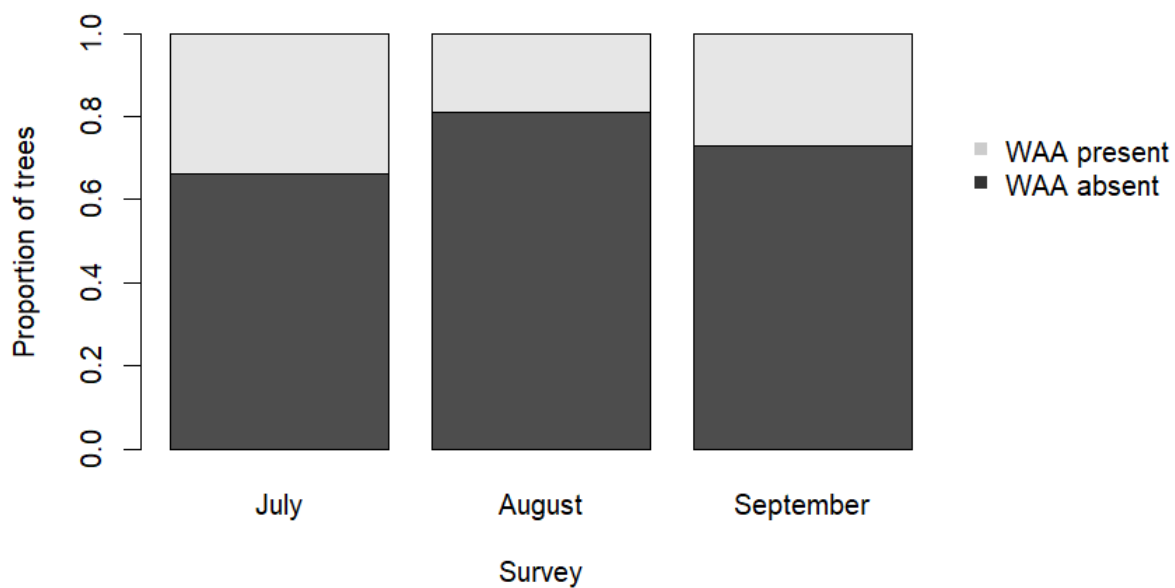


Figure 4-1. The proportion of 200 trees containing WAA during three surveys conducted in 2023.

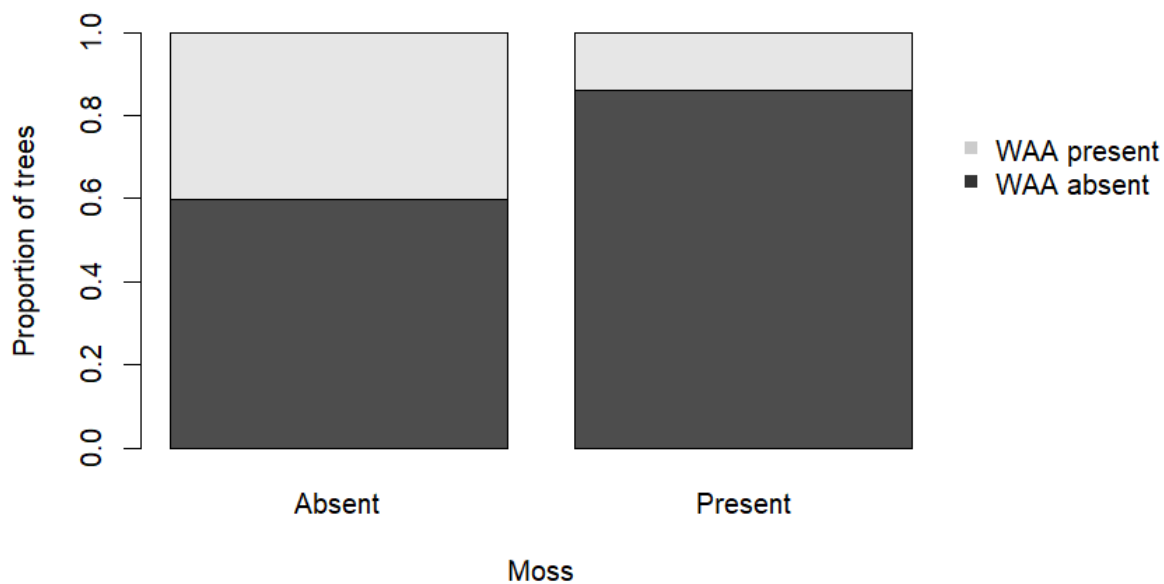


Figure 4-2. The proportion of pseudo-trees containing WAA where moss was either absent ($n = 290$ pseudo-trees) or present ($n = 310$ pseudo-trees) from the row bed. Data were collected in 2023.

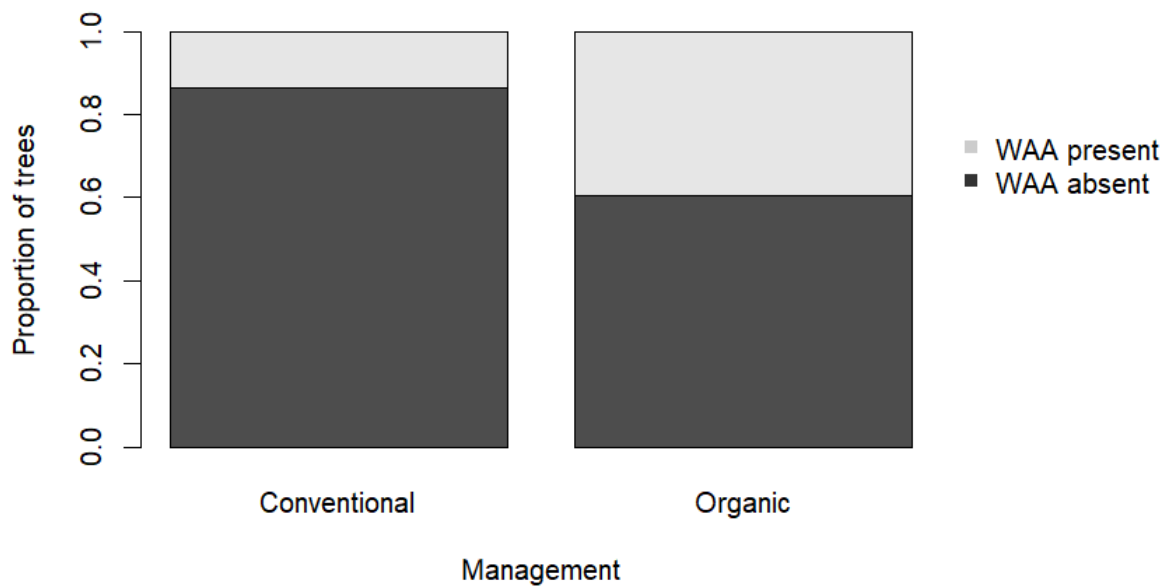


Figure 4-3. The proportion of pseudo-trees which contained WAA which were managed conventionally ($n = 100$ trees, 300 pseudo-trees) or organically ($n = 100$ trees, 300 pseudo-trees). Data were collected in 2023.

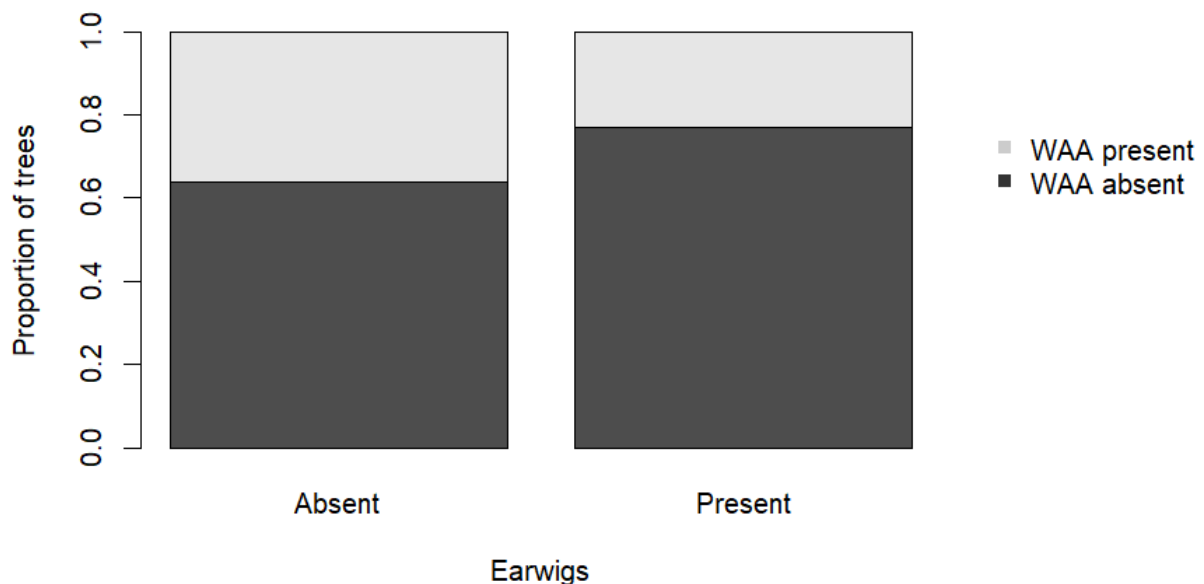


Figure 4-4. The proportion of pseudo-trees which contained WAA where *F. auricularia* was absent ($n = 172$ pseudo-trees) or present ($n = 428$ pseudo-trees). Data were collected in 2023.

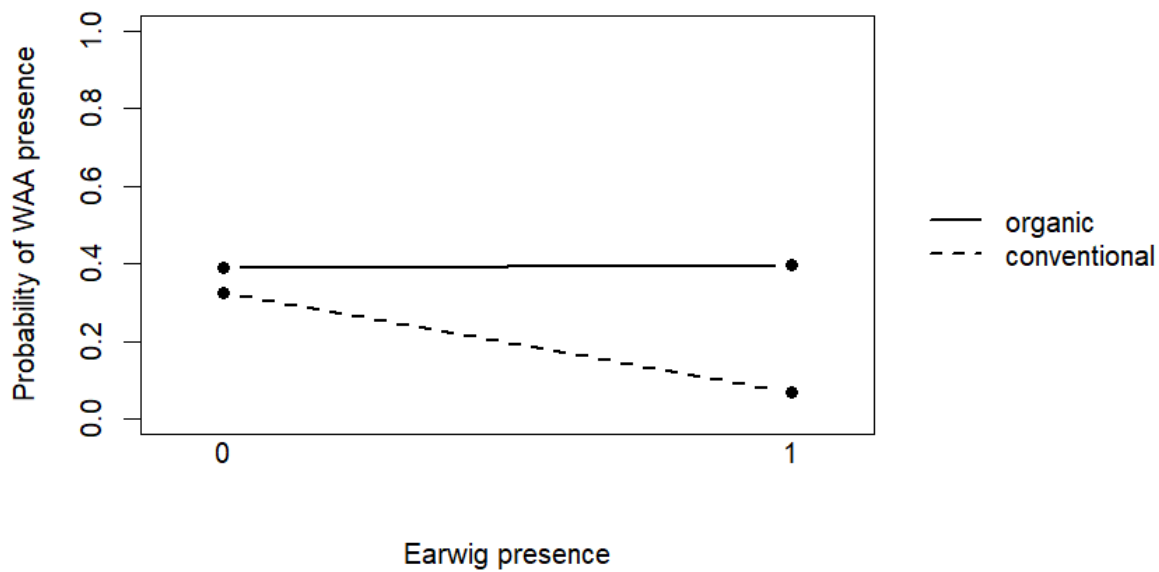


Figure 4-5. The estimated effects of *F. auricularia* (earwig) presence (0 = Absent, 1 = Present) and management style on the probability of finding WAA in a tree. n conventional *F. auricularia* absent = 80 pseudo-trees. n conventional *F. auricularia* present = 220 pseudo-trees. n organic *F. auricularia* absent = 92 pseudo-trees. n organic *F. auricularia* present = 208 pseudo-trees. Data were collected in 2023.

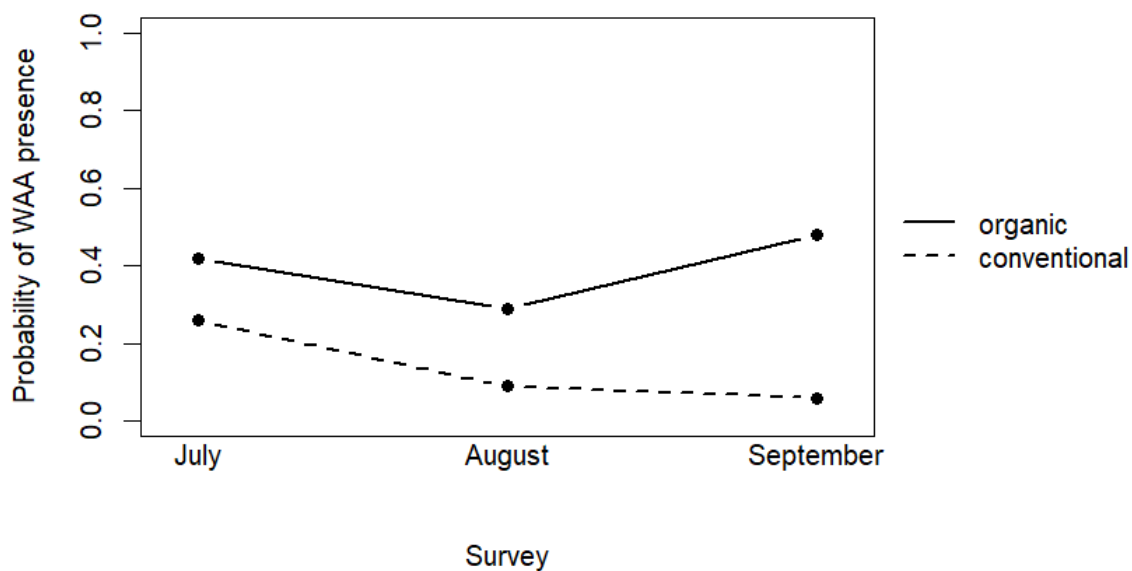


Figure 4-6. The estimated effects of the month a survey was conducted and management style on the probability of finding WAA in a tree. $N = 100$ trees for all 6 datapoints. Data were collected in 2023.

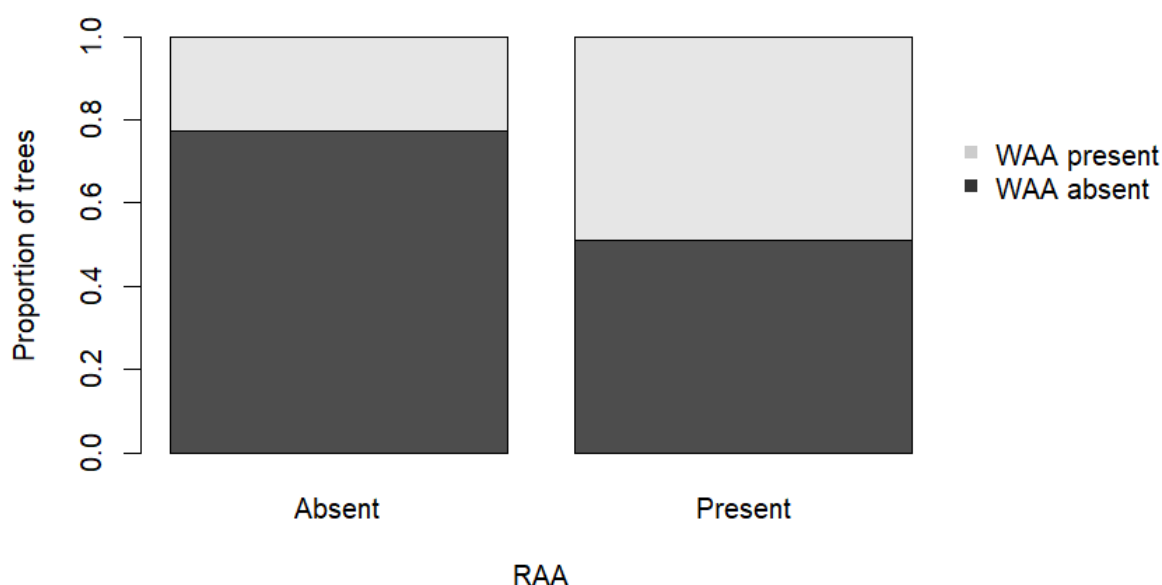


Figure 4-7. The proportion of pseudo-trees which contained WAA where RAA was absent ($n = 508$ pseudo-trees) or present ($n = 92$ pseudo-trees). Data were collected in 2023.

The 2023 Earwig Baseline model (Table 4-3) had the same structure as the WAA Baseline model, with survey as a fixed effect and tree within orchard within grower as nested random effects. This model had an AIC of 407.5; orchard was again the most powerful random effect. The 2023 Earwig Assembled model (Table 4-4) had survey, RAA presence and the abundance of bare earth as fixed effects, and tree as a random effect. The AIC of this model was 558.7. Management style, WAA presence, variety, moss presence, mulch presence, soil type, and plant abundance were all excluded from the model. Changes in the proportion of trees occupied by earwigs during the three months of surveys were observed (Figure 4-8), with the fewest occupied trees in July, the most in August and with September having a similar number of occupied trees to August (although marginally lower). There was a higher likelihood for trees to contain earwigs when the row bed was > 50% bare earth (Figure 4-9). A tree was less likely to contain RAA if earwigs were present (Figure 4-10).

Table 4-3. A model for the presence or absence of *F. auricularia* from 600 pseudo-trees ($n = 200$ trees, 3 surveys). AIC = Akaike Information Criterion. DF = Degrees of Freedom. Std. = Standard.

2023 Earwig Baseline			
AIC	407.5		
Deviance	395.5		
DF residuals	594		
Random Effects			
Name	Type	Variance	Std. deviation
Tree	Intercept	0.6723	0.8199
Orchard	Intercept	10.0218	3.1657
Grower	Intercept	8.6694	2.9444
Fixed Effects			
Name	Estimate	Std. error	<i>p</i> value
Intercept	2.9229	1.6456	0.076
Survey 2	1.0226	0.3619	< 0.01
Survey 3	0.7138	0.3523	< 0.05

Table 4-4. A model for the presence or absence of *F. auricularia* from 600 pseudo-trees ($n = 200$ trees, 3 surveys). AIC = Akaike Information Criterion. DF = Degrees of Freedom. Std. = Standard.

2023 Earwig Assembled			
AIC	558.7		
Deviance	546.7		
DF residuals	594		
Random Effects			
Name	Type	Variance	Std. deviation
Tree	Intercept	15.84	3.98
Fixed Effects			
Name	Estimate	Std. error	<i>p</i> value
Intercept	3.4984	0.8263	< 0.001
Survey 2	1.123	0.3814	< 0.01
Survey 3	0.6849	0.3651	0.061
RAA present	-2.0278	0.7624	< 0.01
Bare earth low	-1.4855	0.4817	< 0.01

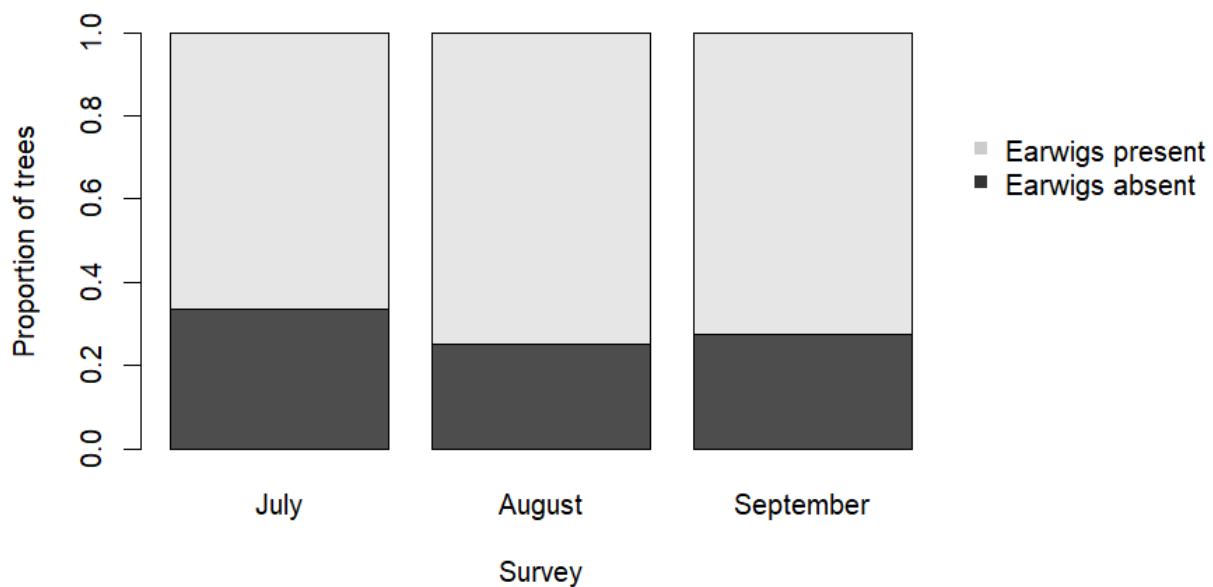


Figure 4-8. The proportion of 200 trees containing *F. auricularia* during three surveys conducted in 2023.

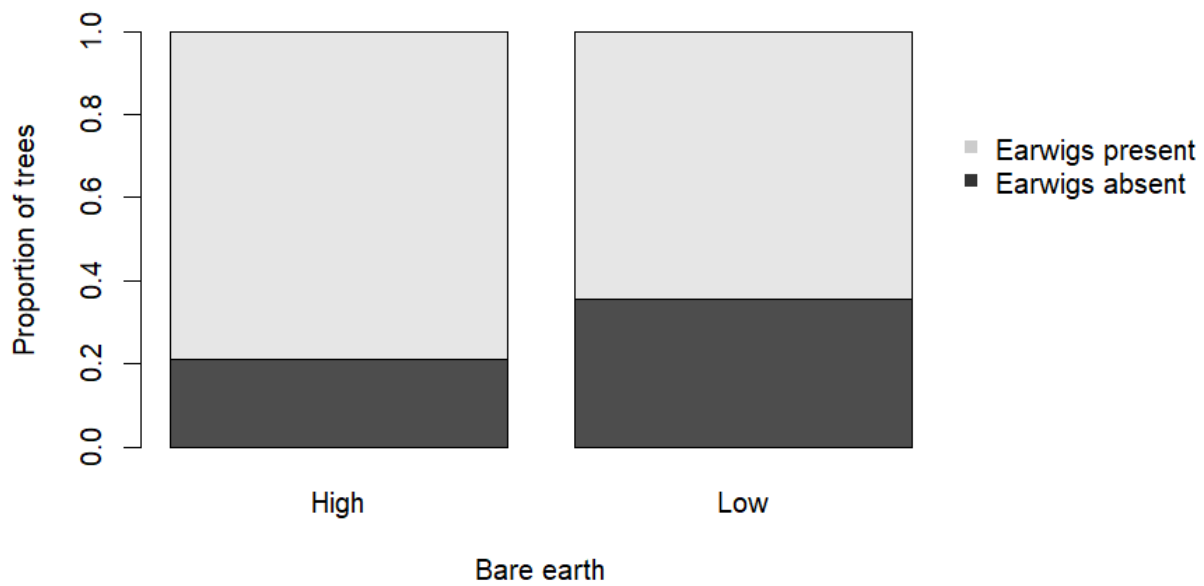


Figure 4-9. The proportion of pseudo-trees which contained *F. auricularia* where the row bed was > 50% bare earth (High; $n = 282$ pseudo-trees, 94 trees) or < 50% bare earth (Low; $n = 318$ pseudo-trees, 106 trees). Data were collected in 2023.

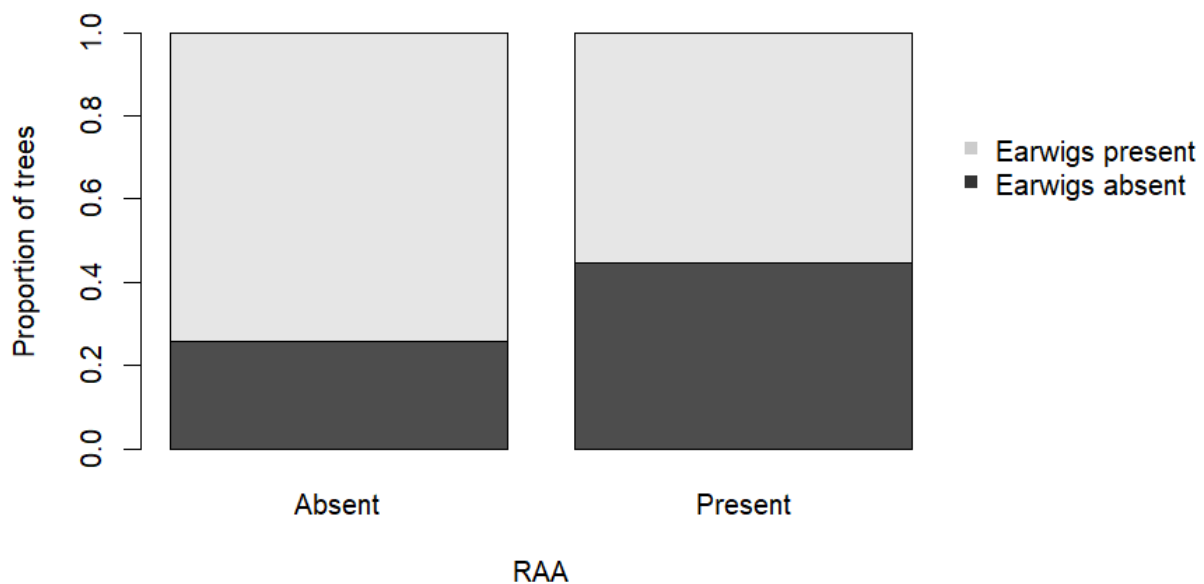


Figure 4-10. The proportion of pseudo-trees which contained *F. auricularia* where RAA was absent ($n = 508$ pseudo-trees) or present ($n = 92$ pseudo-trees). Data were collected in 2023.

Of the 870 earwigs sampled for molecular gut content analysis, 44 (5%) had a positive PCR result. However, when three PCR samples were sent for sequencing, only two returned with close similarity for WAA, while the third was a closer match to *R. padi*. The subsequent PCR test shows that the primer used was not specific to WAA DNA and amplified *R. padi* DNA. All five *R. padi* DNA samples were amplified by the primers during PCR. It is therefore impossible without further sequencing to say how many of the 44 positive samples were from earwig consumption of WAA.

4.2. Impact of artificial shelters on the numbers of earwigs and *Eriosoma lanigerum* in an experimental apple orchard

4.2.1. Earwig assessment

There was no significant difference in the number of earwigs in the apple tree canopies at night between the blocks (3, 5, and 6) with no artificial shelters (Kruskal-Wallis test: $df = 2$, $H = 3.47$, $p = 0.18$; Figure 4-11).

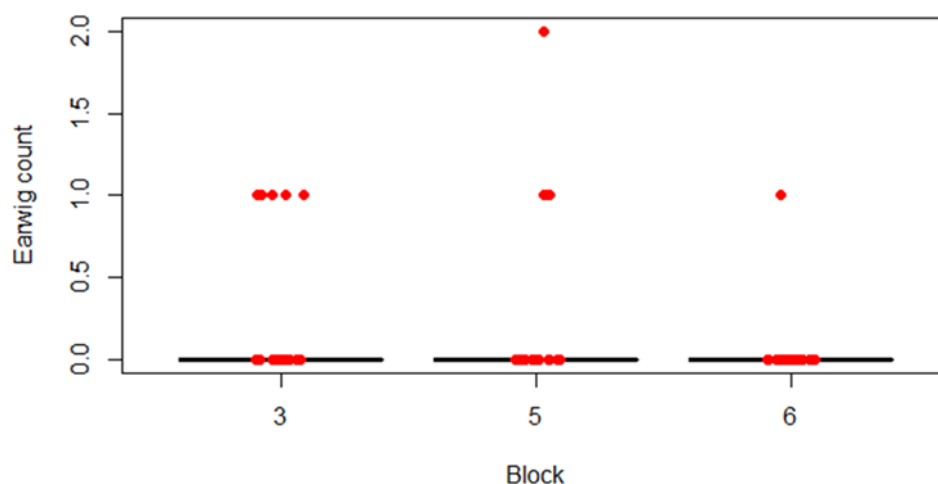
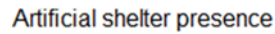


Figure 4-11. Earwig (*Forficula auricularia*) counts from Royal Gala apple (*Malus domestica*) trees in different orchard blocks which did not contain artificial *F. auricularia* shelters ($n = 22$ in all cases). Datapoints are superimposed in red.

When the effect of artificial shelters was tested, significantly more earwigs were recorded on apple trees with shelters (Wilcoxon test: n without shelter = 22, n with shelter = 22, $W = 59$, $p < 0.001$; Figure 4-12). This test was completed by comparing Block 6 to Block 7, due to the similarity in their history of insecticide treatment (Table 3-3). However, given that the different untreated blocks did not have significantly different numbers of earwigs (see above), a second analysis was done comparing Block 7 to all other blocks.



Artificial shelters were associated with significantly higher numbers of earwigs in apple trees at night (Wilcoxon test: n without shelters = 66, n with shelters = 22, $W = 214.5$, $p < 0.001$; Figure 4-13).

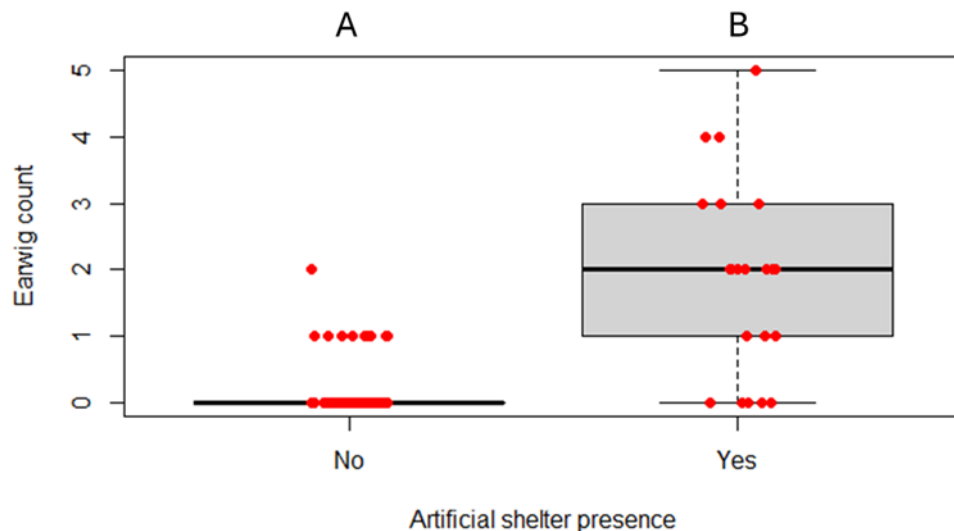


Figure 4-13. Earwig (*Forficula auricularia*) counts from Royal Gala apple (*Malus domestica*) trees in orchard blocks which either did ($n = 22$) or did not ($n = 66$) have artificial shelters for *F. auricularia*. These data come from orchard blocks with various histories of insecticide use. Datapoints are superimposed in red. Groups which do not share a letter are significantly different ($p < 0.05$).

4.2.2. Woolly apple aphid assessment

When comparing the WAA colony count of Block 7 (artificial shelters) with Block 6 (no artificial shelters), the addition of artificial shelters appeared to have no significant effect (Wilcoxon test: n without shelters = 22, n with shelters = 22, $W = 254.5$, $p = 0.78$; Figure 4-14). These blocks were selected for comparison due to their similar histories of insecticide treatment (Table 3-3).

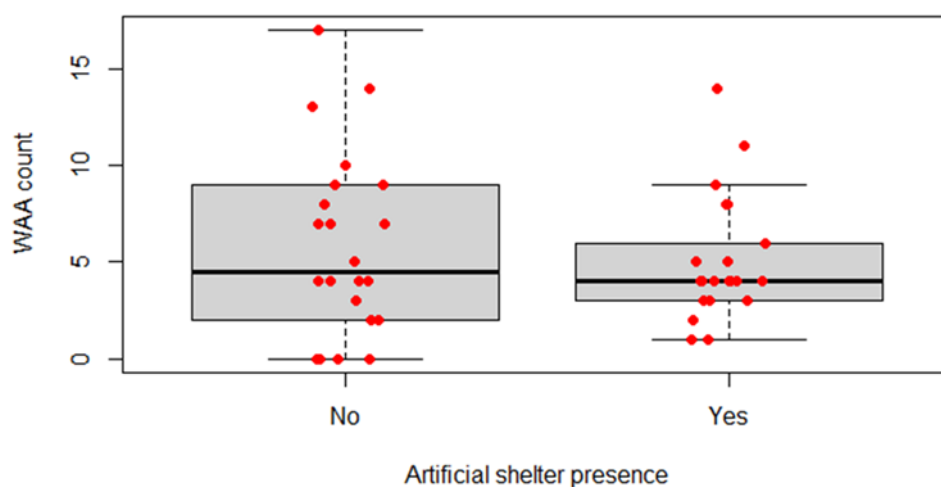


Figure 4-14. Woolly apple aphid (*Eriosoma lanigerum*) colony counts from Royal Gala apple (*Malus domestica*) trees in orchard blocks which either did ($n = 22$) or did not ($n = 22$) have artificial

shelters for *F. auricularia*. These data come from blocks with similar histories of insecticide use. The datapoints are superimposed in red.

When comparing orchard blocks without artificial shelters, there were significant differences between blocks (Kruskal-Wallis test: $df = 2$, $H = 24.65$, $p < 0.001$; Figure 4-15). Post-hoc testing showed that Block 3 had significantly higher numbers of WAA colonies than Block 5 ($p = 0.025$) and Block 6 ($p < 0.001$) but Blocks 5 and 6 were not significantly different ($p = 0.061$). Block 7 was excluded from this analysis.

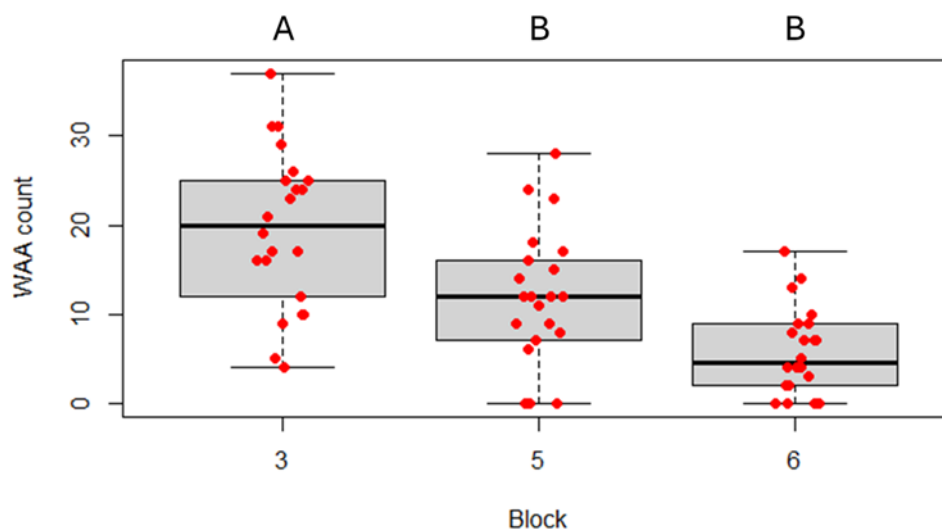


Figure 4-15. Woolly apple aphid (*Eriosoma lanigerum*) colony counts from Royal Gala apple (*Malus domestica*) trees in orchard blocks with different histories of insecticide use. These data include only blocks without artificial shelters. The datapoints are superimposed in red. Groups which do not share a letter are significantly different ($p < 0.05$).

Given the presence of artificial shelters did not appear to have a significant effect on the WAA colony count (Figure 4-14), it is also possible to conduct a Kruskal-Wallis test that includes Block 7, thus comparing all blocks. This test showed there were significant differences between the blocks in WAA counts (Kruskal-Wallis test: $df = 3$, $H = 36.03$, $p < 0.001$; Figure 4-16). Post-hoc analysis showed that the trees in Block 3 had significantly higher WAA colony counts than Block 6 ($p < 0.001$) and Block 7 ($p < 0.001$), and Block 5 had significantly higher WAA colony counts than Block 7 ($p < 0.05$). Blocks 3 and 5 were not significantly different ($p = 0.076$), neither were Blocks 5 and 6 ($p = 0.090$), or Blocks 6 and 7 ($p = 1.00$).

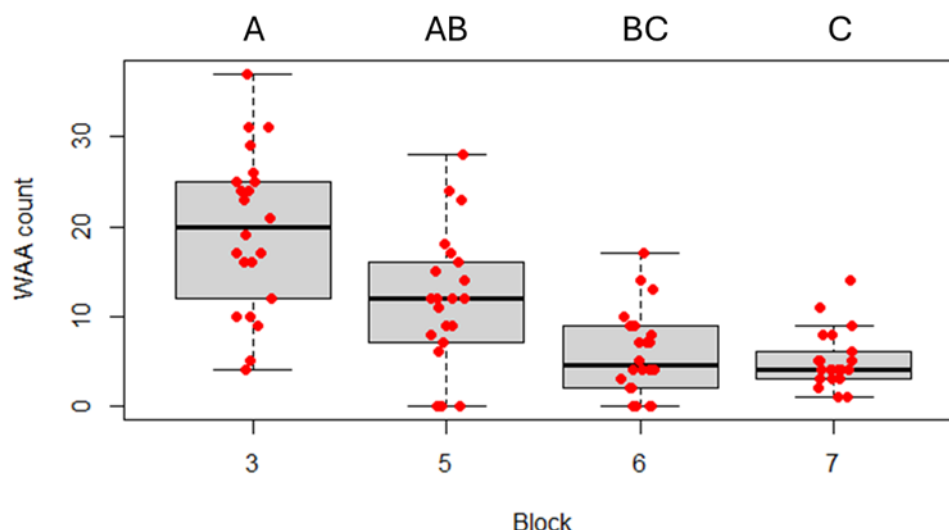


Figure 4-16. Woolly apple aphid (*Eriosoma lanigerum*) colony counts from Royal Gala apple (*Malus domestica*) trees in orchard blocks with different histories of insecticide use. These data include a mix of blocks with and without artificial shelters. The datapoints are superimposed in red. Groups which do not share a letter are significantly different ($p < 0.05$).

The highest numbers of WAA were found in descending order in Blocks 3>5>6>7 (Figure 3-7). The respective insecticide toxicity scores for WAA were 28, 28, 37, 37 (Table 3-3) and hence WAA colony count per tree did not seem to be related to past insecticide applications.

4.3. Radio frequency identification mesocosm designs for the study of earwig behaviour

4.3.1. Mortality

The best generalized linear model for mortality included only treatment as a factor. Sex, the duration spent in the bee marking cage, and the weight of an individual at the start of the experiment (pre-treatment) were not significant factors for mortality. A Fisher test confirmed there were significant differences in mortality between the treatments ($p < 0.001$). However, post-hoc pairwise analyses of the different treatments showed no individually significant comparisons ($p > 0.05$ in all cases). This is likely due to the high number of treatments relative to the number of individuals per treatment. Despite this lack of significant pairwise comparisons, there are very clear effects on mortality by treatment (Figure 4-17). The only deaths which occurred during the experiment were earwigs which were treated with one of the two cyanoacrylate glues. When looking at the glues alone (without a tag being applied), four of the 10 earwigs treated with Gorilla glue, and five of the nine earwigs treated with Gorilla gel, died, *i.e.* both cyanoacrylate glues caused a close-to-50% mortality rate when applied alone. However, when applied with tags, a

single earwigs treated with Gorilla gel died (out of 10), and none of the 10 earwigs treated with Gorilla glue (and a tag) died.

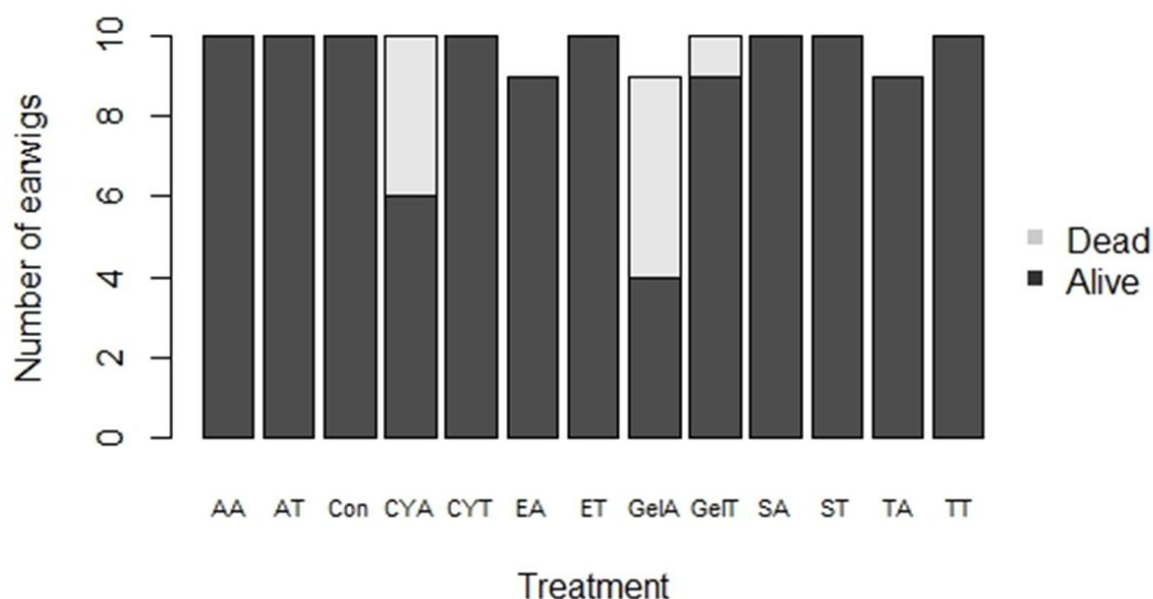


Figure 4-17. The number of *F. auricularia* which either survived or died following a given treatment during a fourteen-day experiment. The treatment codes stand for the following: AA = Araldite alone, AT = Araldite with tag, Con = Control, CYA = Gorilla glue alone, CYT = Gorilla glue with tag, EA = Eyelash glue alone, ET = Eyelash glue with tag, GelA = Gorilla gel alone, GelT = Gorilla gel with tag, SA = Shellac alone, ST = Shellac with tag, TA = Thermoplastic glue alone, TT = Thermoplastic glue with tag.

4.3.2. Tag retention

For tag retention, sex and the weight prior to the experiment were not significant. The best model showed glue and the time spent in the bee marking cage as significant ($p < 0.05$), with an interaction between these two factors. A pairwise Wilcoxon test on the number of days tagged for each glue found that both cyanoacrylates had significantly higher median days tagged than araldite, shellac, and the eyelash/latex ($p < 0.05$ in all cases). Thermoplastic glue had significantly higher tag retention than the eyelash/latex ($p < 0.01$). All other pairwise comparisons were not significantly different ($p > 0.05$ in all cases). This showed that in order from most to least effective the glues were ranked Gorilla glue = Gorilla gel > thermoplastic glue > Araldite = shellac > eyelash glue (Figure 4-18). Time spent in the bee marking cage was negatively correlated with the number of days a tag remained attached, which had an interaction with glue type. Figure 4-19 shows that the model predicted Araldite and shellac to perform better as time spent in the bee marking cage trended towards 0.

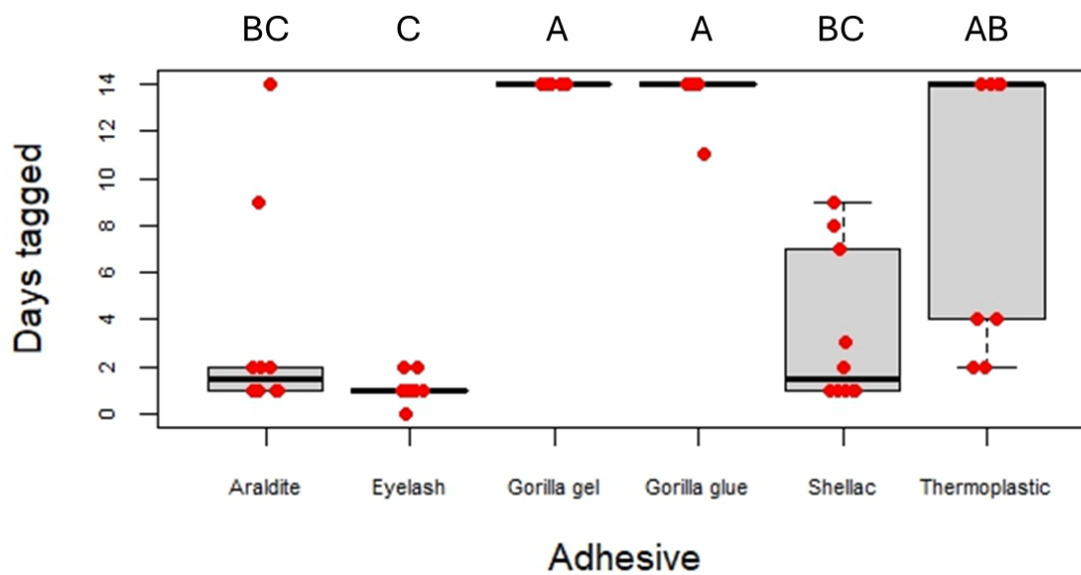


Figure 4-18. The number of days tags remained attached to *F. auricularia* using various glues. The datapoints are superimposed in red. Treatments which do not share a letter are significantly different ($p \leq 0.05$). $N = 10$ for all treatments apart from Gorilla gel where $N = 9$. The experiment ended after fourteen days.

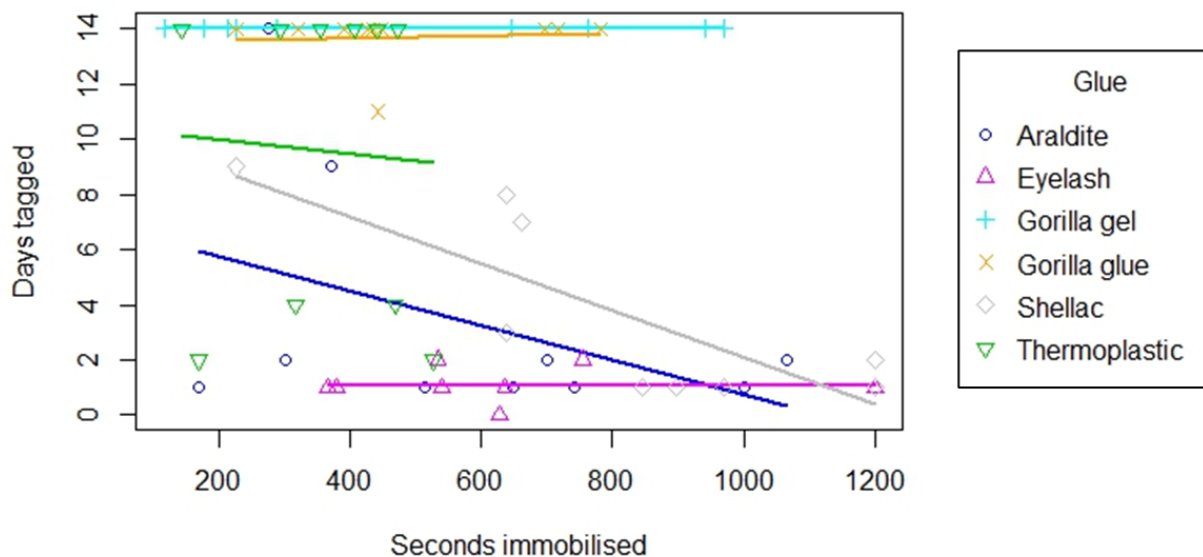


Figure 4-19. The predicted relationship between the time spent immobilised in a bee marking cage and the number of days a tag remained attached to a *F. auricularia* for different glues, based on a negative binomial generalized linear model. $N = 10$ for all treatments apart from Gorilla gel where $N = 9$. The experiment ended after fourteen days.

5. Discussion

5.1. Earwigs and *Eriosoma lanigerum*

This study demonstrated that earwigs were a contributor to the control of WAA. This is in agreement with many other studies which have shown the efficacy of earwigs for control of WAA (Stap *et al.*, 1987; Mueller, Blommers & Mols, 1988; Nicholas, Spooner-Hart & Vickers, 2005; Quarrell, Corkrey & Allen, 2017; Alins *et al.*, 2023).

While the scope of this study was not as large as Happe *et al.* (2018) or Helsen *et al.* (2007), the survey work included more orchards than other previous surveys on earwigs and WAA. This is important given that the main concern with earwig control of WAA is its inconsistency. The results of this study are supported by Helsen *et al.* (2007), but contrary to the findings of Happe *et al.* (2018). The approach taken of using presence and absence rather than true abundance of each species was important for allowing the comparison of so many orchards; orchards could be included even when they had a very low abundance of WAA or earwigs. However, this also means that only total elimination of detectable WAA from a (pseudo)tree was considered. This is a stringent definition to use for control, so the presence of a detectable effect on WAA is a strong indicator of the value being provided by earwigs. However, it may lead to an underestimation of the value of earwigs, particularly in organic orchards, and thus bias the models towards the detection of interaction effects.

The role of management type in the modelling was of key importance. The lack of an impact of management type on earwig presence is important (discussed further below), as is the finding of more WAA-infested trees in the organic orchards compared to conventional orchards. Woolly apple aphid is sometimes considered most serious in orchards which have been sprayed with broad-spectrum insecticides, the theory being that WAA is released from control by its natural enemies (Alspach & Bus, 1999; Heunis & Pringle, 2003; Nicholas, Spooner-Hart & Vickers, 2005; Beliën *et al.*, 2010; Wearing, Attfield & Colhoun, 2010; Goossens *et al.*, 2011; Beers, Horton & Miliczky, 2016). The bias from using presence/absence must be considered; the presence of more WAA infested trees in organic orchards does not actually mean WAA was economically damaging, as it may have been at low enough abundance to not impact the tree or fruit.

The finding that earwigs appeared to be effective at eliminating WAA from trees only in conventionally managed orchards is novel. This may be an indicator of the efficacy of spirotetramat (or flonicamid) in controlling WAA in tandem with earwigs. These insecticides are also not directly

harmful to earwigs, so may be compatible with biological control of WAA (Shaw and Wallis, 2010; Vogt, Just, and Grutzmacher, 2010). Gontijo, Beers and Snyder (2015) suggested supplementary control from a second source was required to make earwigs effective at WAA control. This highlights that earwigs' lack of specificity to WAA allows it to be present before WAA is established and therefore attack the most vulnerable stages of the lifecycle.

The evidence for earwig control of WAA in this study comes from populations of earwigs which had not been experimentally manipulated to enhance contrasts. There was no removal or release of earwigs (other than the replacement of individuals taken for molecular gut content analysis). Hence this study may improve grower confidence in the efficacy of naturally-occurring earwigs and indicate that with the correct management (*e.g.* minimal harmful insecticide sprays and no tillage while earwigs are overwintering; Fountain & Harris, 2015), expensive augmentative releases to control WAA might not be necessary. That being said, the earwig populations in the orchards were monitored using refuge trapping (see below).

The finding of this study suggests that artificial shelters can lead to increased earwig abundance. This supports the findings of Moerkens *et al.* (2009), Jana *et al.* (2021) and Bischoff (*pers. comm.*). The implications of this for earwig distribution are discussed below. This also has implications for the interpretation of previous research conducted using refuge trapping. If the provisioning of artificial shelters for earwigs enhances their abundance in trees, then studies relying on refuge trapping will tend to overestimate earwig abundance in apple orchards, particularly later in the season. This may also bias studies (such as our own) which use refuge trapping to investigate earwig and WAA interactions towards overestimating the effect of earwig populations on WAA. In orchards without artificial shelters, earwigs may not be as effective at controlling pests. While this study did not find evidence for it, the provision of shelter alone may serve to enhance the control of WAA by earwigs.

In this study the rate of earwig predation of WAA in apple trees was analysed using molecular gut content analysis. In this study the rate of detectable WAA DNA was very low, only 5%, when compared with that of previous studies (23 – 30%; Romeu-Dalmau, Piñol & Agustí, 2012; Orpet *et al.*, 2019a). This could either be the result of problems with the methodology reducing the detectability of WAA DNA or reflect a real frequency of predation lower than those encountered in other studies.

To address the methodology, aphid DNA will be most easily detectable in the guts of earwigs immediately following predation. From this point onwards the probability of detecting WAA DNA will exponentially decay (Greenstone *et al.*, 2007). Because earwigs feed at night, but were captured

during the day, there is the potential for a lengthy period of DNA decay before the samples are collected. The methodology used was updated between years to try and minimise this period, by collecting samples for molecular gut content analysis early in the morning, and by placing earwigs immediately onto ice. When placed onto ice, earwigs from a given tree were put into a plastic bag, which was placed inside a plastic tube to prevent crushing, with the tube being pushed into the ice. There would therefore be some degree of insulation from the cooling of the ice, which may have reduced the effectiveness of this procedure for preserving DNA. Certainly the earwigs were not cooled sufficiently to kill them until they were returned to the laboratory and placed into a -80 °C freezer. However, even a small degree of cooling should substantially slow the earwigs' digestion process (Cossins, 1987; Schulte, 2015). There was also the potential for the dissection procedure to contribute to low detection; 1) earwigs were dried but not washed after immersion in 5% bleach giving the potential for bleach to degrade DNA, although it seems unlikely there was significant penetration of bleach in the gut, 2) During dissection earwigs were thawed to room temperature, for up to 8 hours. The periodic returning of dissected guts to the freezer, and collection of new individuals for dissection closer to the time they were required, may have helped preserve detectable WAA DNA, 3) There may have been a reduction in the detectability of DNA during the tissue homogenisation and lysis steps of the DNA extraction. Manual grinding of earwigs using a micropestle may have been more effective than the use of a Geno/Grinder (Erica Moretti, Rebecca Schmidt-Jeffries, *pers. comm.*). The three-hour lysis step could be extended further to allow more complete lysis. Improvements in these areas would release more DNA from tissue, allowing it to be extracted and detected more effectively.

If the low level of detectable DNA in the molecular gut content analysis is assumed to reflect a true low frequency of predation, it is unclear why it was lower in the present study than in those carried out by Orpet et al. (2019a) and Romeu-Dalmau, Piñol and Agustí (2012). Romeu-Dalmau, Piñol and Agustí (2012) used non-species-specific aphid primers, and so the higher frequency of DNA detection in their study might be explained by the broader range of detectable DNA. Orpet et al. (2019a), however, used the same primers (ostensibly WAA specific, discussed further below). The study location of Washington has a warmer climate than in this study; potentially this has implications for the duration of active foraging by earwigs, or the speed of searching and predation. The four orchards used by Orpet et al. (2019a) for their study were also all organic, so potentially WAA was more abundant and therefore more likely to be encountered and predated by earwigs. It is worth noting that across 2022 and 2023, 944 samples, or 1,237 earwig individuals, were processed. By comparison, Orpet et al. (2019a) sampled 315 earwigs and Romeu-Dalmau, Piñol and Agustí (2012) sampled 96.

During the molecular gut content analysis, the primer used was also found to be non-species-specific, making the results of the molecular gut content analysis much less informative on earwig and WAA interactions. We found the primer also amplified *Rhopalosiphum padi* DNA. Further testing should be done for other aphid species. Orpet *et al.* (2019a) did not indicate how common *R. padi* was in US apple orchards, so it is unclear if this would affect their results. It is also important to note that primers have the potential to non-specifically bind across kingdoms, not just species (Farwell, *pers. comm.*). Careful consideration must therefore be taken in their design. Databases can be used to predict the specificity of primers; however, these databases are limited by the information available at the time of using. As the *R. padi* genome was not submitted to the National Center for Biotechnology Information database until 2021, it is entirely possible that Orpet *et al.* (2019a) missed this potential off-target due to the lack of available data.

The negative effect of moss presence in the row bed of apple orchards on WAA presence in the 2023 modelling was unexpected. To the author's knowledge, no similar interaction has been recorded before. A direct interaction between moss and WAA seems unlikely, even for edaphic WAA which would be closer to the surface of the row bed. As mosses tend to prefer shaded and damper conditions, there is a potential that the presence of moss correlates with a microhabitat variable such as shading, soil temperature, moisture, or the level of irrigation. These could in turn have a significant impact on the rate of WAA reproduction and nymphal development.

5.2. Earwig association with orchard and tree factors

This study was unable to identify many factors strongly linked to the presence of earwigs in orchard trees. Previous research has often found earwig populations are highly variable and difficult to predict (Phillips, 1981; Burnip *et al.*, 2002; Gobin *et al.*, 2006, 2008b; Moerkens *et al.*, 2009). It seems likely that given the temperature-dependent nature of earwig development, this variability will become more extreme with climate change. Although some previous researchers have found a high degree of within-orchard variation in earwig abundance (Gobin *et al.*, 2006), the baseline models in this study suggested that inter-tree variation was less important than inter-orchard variation. Variation between growers was similarly less important than inter-orchard variation. In one of the orchards surveyed in 2023 there were 1,477 earwigs caught in the refuge traps across all three surveys. The two other orchards owned by the same grower had 0 and 15 earwigs.

Earwigs were not significantly more abundant in the organic orchards compared to the conventional orchards. This is contrary to some previous studies (Helsen *et al.*, 2007; Logan, Maher & Connolly, 2011; Malagnoux *et al.*, 2015), but corroborated by others (Nicholas, Spooner-

Hart & Vickers, 2005; Happe *et al.*, 2018). It has been speculated that increased tillage in organic orchards might cancel out any benefit from reduced insecticide use in organic orchards (Happe *et al.*, 2018; Biscoff, *pers. comm.*). Alternatively, it may be that organic orchards support a greater diversity and abundance of competitors to earwigs (other generalist predators), again cancelling out the reduced insecticide pressure. This is beneficial for growers, as it implies that all growers can benefit from earwigs as a natural enemy of WAA and other pests.

There were no strong correlations between earwig presence and any of the alternative food sources tested in the study, such as moss and algae. This is perhaps unsurprising given the highly polyphagous nature of earwigs (Crumb, Bonn & Eide, 1941; Lamb & Wellington, 1975; Phillips, 1981). It seems unlikely that earwig presence would be dictated by access to any one food source, and indeed in all apple orchards the trees themselves will provide a plentiful alternative food source for earwigs. This may mean that, in apple orchards, factors besides food availability are more important in dictating the presence and abundance of earwigs.

This study did find a significant positive effect of a high proportion of bare earth in the row bed on earwig presence. This was slightly unexpected, as flowering plants or moss cover should act as alternative food sources for earwigs. However, as outlined above, this may not be a limiting factor in apple orchards. Instead, bare earth might be correlated with higher soil temperatures when earwigs are still sheltering in brood chambers, either during winter or spring (Yu *et al.*, 2022). Temperature has been shown to play an important role in the development of earwig eggs and nymphs (Atwell, 1927; Lamb, 1974; Phillips, 1981). Previous research has shown the timing of earwig emergence from underground nests can vary by up to a month depending on the temperature (Moerkens *et al.*, 2009). Roots from plant cover may also physically inhibit the excavation of brood chambers (Tsiolis *et al.*, 2022). This explanation does assume, however, that earwigs are nesting in the row bed, something which may be contentious. Further investigation into soil characteristics, in particular drainage, seems warranted.

It has been proposed that earwigs overwinter outside orchards in Mediterranean citrus orchards (Romeu-Dalmau, Espadaler & Piñol, 2016). This would imply a seasonal migration of earwigs into and out of orchards each year, something which has not been observed. Other studies have shown that earwigs appear to be fairly sedentary within an orchard, moving less than 30 meters over the span of a month (Phillips, 1981; Moerkens *et al.*, 2010). It seems unclear to what degree earwigs in tree fruit orchards are influenced by the surrounding landscape. Traditionally, it has been thought that earwigs have poor dispersal under their own power (Crumb, Bonn & Eide, 1941). Part of this is that flight has been largely dismissed as an important factor in earwig dispersal. However, it seems clear that under certain (uncharacterised) conditions, earwigs will fly in large

numbers (Buzzetti *et al.*, 2003; Pavón-Gozalo *et al.*, 2011). To the author's knowledge, this has never been observed in an agricultural landscape, but even in the absence of flight, dispersal between orchards and the surrounding landscape may be more important than has generally been accepted. Studies investigating the influence of landscape factors on earwig abundance have broadly shown a lack of significant relationships; however, interactions with nearby woodland or hedgerow (both positive and negative) are sometimes significant (Debras *et al.*, 2007; Malagnoux *et al.*, 2015; Happe *et al.*, 2018). Similarly, several studies demonstrate earwigs have a strong ability to recolonise orchards sprayed with broad-spectrum insecticides (Nicholas, Thwaite & Spooner-Hart, 1999; Malagnoux *et al.*, 2015; Simon *et al.*, 2024). This implies dispersal of earwigs into the orchards from surrounding areas. There is a lack of information on the status of earwig populations within more natural environments. There are reports that it prefers grassland and shrubs to woodland, that it has been found in coniferous forests, and that it prefers human-disturbed habitats; which is to say that there appears to be mixed information on the habitat preferences of earwigs (Kocarek, 1998; Pavón-Gozalo *et al.*, 2011; Hill *et al.*, 2019). It may be that an understanding of earwig population dynamics within apple orchards is incomplete without an understanding of populations in the surrounding environment.

Subspecies of earwigs have been infrequently distinguished in the literature by the number of broods produced (Lamb & Wellington, 1975; Phillips, 1981; Wirth *et al.*, 1998; Guillet *et al.*, 2000; Hill *et al.*, 2019). However, studies have shown subspecies-specific differences in dispersal and cold tolerance, implying that the subspecies of earwig may differ in other important aspects of their biology (Moerkens *et al.*, 2010, 2012). It may be important to begin contextualising the results of earwig research with the subspecies the research was completed on. This likely has not been carried out thus far because firstly, the subspecies cannot be visually differentiated, and secondly, multiple subspecies often occur sympatrically within orchards (Guillet *et al.*, 2000; Moerkens *et al.*, 2009; Quarrell *et al.*, 2018; González Miguéns *et al.*, 2020).

This study adds to the small but growing body of evidence that the availability of shelter may be an important population-limiting factor for earwigs in apple orchards (Moerkens *et al.*, 2009; Jana *et al.*, 2021; Bischoff, *pers. comm.*). The addition of artificial shelters cannot lead to increased reproduction within the year of introduction, due to the length of the earwig lifecycle. Artificial shelters may either reduce mortality, leading to a true increase in earwig abundance, or concentrate earwigs into trees where shelters have been added, leading to a change in distribution without increasing abundance. In the latter, there should be a concurrent decrease in earwig abundance in the surrounding area, as earwigs aggregate in trees with artificial shelters provided. This would have implications for the as-yet unexplained population crash upon moulting from 5th instar into adults (Moerkens *et al.*, 2009). While Moerkens *et al.* (2009) were unable to identify a

causal mechanism, they showed that the degree of mortality from 5th instar to adulthood is density-dependent, with increased mortality at higher densities. As stated, this study and others have shown an apparent increase in earwig abundance thanks to shelters (Moerkens *et al.*, 2009; Jana *et al.*, 2021; Bischoff, *pers. comm.*); however, these studies have been conducted over a single year. If artificial shelters merely concentrate earwig populations (see above), then they may lead to a long-term decline in earwig abundance by increasing density-dependent mortality. Studies investigating the impact of artificial shelters over multiple years should be conducted.

If, instead, mortality is being reduced by artificial shelters, then this could be due to protection from hazardous environmental conditions (e.g. protection from desiccation), or protection from predation (Crumb, Bonn & Eide, 1941; Lamb, 1975). Lamb (1975) believed the key benefit of artificial shelters to earwigs was a reduction in predation by birds. However, Peusens *et al.* (2009) found no clear effect of bird exclusion on earwigs, and while the effect of bird exclusion was not a research question in Marshall and Beers (2021, 2022) experiments, their exclusion netting presumably excluded birds, and they did not find a significant increase in earwig abundance inside of netted blocks. Older literature has mentioned starlings (*Sturnus vulgaris*; L.) as a potentially important predator of earwigs, but this appears to be based mainly on observation rather than empirical testing (Crumb, Bonn & Eide, 1941; Phillips, 1981). Predation by birds was one of the mechanisms put forward to explain the density-dependent population crash (Moerkens *et al.* 2009). If this is the case (and artificial shelters protect from birds) then rather than a long-term decline (see above), artificial shelters should lead to a long-term increase in earwig abundance. The role of predation in earwig population ecology should be investigated further.

The presence of density-dependent mortality in a species which actively aggregates is a challenge to explain, and calls into question what benefits earwigs derive from aggregating. Another of the mechanisms proposed for density-dependent mortality by Moerkens *et al.* (2009) was cannibalism, but this seems even more contradictory to the benefits of aggregation than factors such as predation, disease, or attack by parasites/parasitoids. Almost all study of cannibalism in earwigs have been conducted on populations held in the laboratory while they are in the ‘family’-living stage of their lifecycle (Dobler & Kölliker, 2010, 2011; Wong & Kölliker, 2013; Wong, Lucas & Kölliker, 2014; Van Meyel & Meunier, 2020). The importance of cannibalism once earwigs have begun to occupy tree canopies and have dispersed from their family units is unknown. If conspecifics did pose a significant risk to earwigs then the tendency to seek out occupied shelters would appear to be maladaptive. While a high degree of mortality because of moulting failures seems likely (Fountain, *pers. comm.*), this and weather conditions would be expected to cause a flat rate of mortality independent from the population density of earwigs.

5.3. Radio frequency identification

Given the many unknowns about earwig biology in the field, a remote monitoring system that could help track individuals and determine their fate would be desirable. Current RFID technology means that tags small enough to attach to earwigs will likely need to be paired with static RFID antennas. Passive RFID tags for use with mobile antennas tend to be heavier (up to 50% of earwig adult body mass; Pope *et al.*, 2015; own data). Artificial shelters with RFID readers at the entrance/exit might be capable of repeatedly detecting earwigs in the field; as they will return to the same refuge on multiple nights if food is nearby (Lamb, 1975). However, given the apparent lack of fidelity for a refuge (Lamb, 1975), large numbers of tagged individuals (or RFID antennas) might need to be released in order to generate sufficient data. This may make RFID monitoring of earwigs in the field prohibitively expensive, but this has not been explored. Compounding this is the difficulty of attaching tags to earwigs; they appear naturally suited to removing tags.

Remote monitoring using mesocosms, in the laboratory or field, may provide a way to compensate for the shortcomings of fixed antennas. Robust datasets could be generated from smaller numbers of tagged individuals, and the rate of tag loss can be monitored. There are a number of interesting avenues of enquiry for the study of earwig behaviour using mesocosms, and such studies would be (to the author's knowledge) the first of their kind conducted on a sub-social insect. Foraging behaviour is still poorly understood, and mesocosm-based remote monitoring studies might be able to answer questions such as:

- Do earwig individuals forage multiple times in a night?
- Do earwigs deliberately vary their diet, and if so, over what durations of time does this occur?
- Is protein-rich insect prey preferred over vegetable food sources?
- Do earwigs learn to navigate their immediate surroundings with greater speed over time?

Another interesting area to explore is the social dynamics of earwigs after the brood-tending stage. Pro-social behaviour has been reported while earwigs shelter, but anti-social behaviour has been reported while feeding (Lamb, 1975). To the author's knowledge, only Lamb (1975) has studied dominance hierarchies of earwigs while feeding. A remote monitoring mesocosm study capable of identifying individuals, such as RFID, might be able to shed more light on this topic, in particular in relation to population density. A study which investigated the benefits and costs of aggregation at variable densities might also provide useful information on the density-dependent mortality discussed above.

This study provided some of the first information on the feasibility of tagging earwigs, which could be useful both for RFID and video monitoring techniques. Cyanoacrylates, the most commonly used glues when attaching tags to insects, appear to be toxic to earwigs, as has been found for

multiple other species (Boiteau et al., 2009, 2010; Pope et al., 2015; Kirkpatrick et al., 2019; Toppa et al., 2020). Thermoplastic glue appears to be the best-performing alternative that did not induce mortality during the experiment, although tag retention was lower for thermoplastic glue than for cyanoacrylates. Further work could investigate sublethal effects of tagging on earwigs, such as possible reductions in the speed of movement or vertical climbing ability (Kaláb et al., 2021). Evidence of tag-induced changes in behaviour, namely what appeared to be deliberate tag scraping, was observed. This highlights that even when there are no observable changes in mortality or mobility, tagged animals may still be affected behaviourally. There did not appear to be an additive effect from the weight of tags and the toxicity of cyanoacrylate glue on earwig mortality. This goes against other research on the topic, and may thus be an artefact of the low replication in this study (Pope et al., 2015; Toppa et al., 2020). Further investigation may be warranted to understand tag-glue interactions.

Given the weight of evidence, the author would strongly advise researchers glueing tags to insects to consider avoiding cyanoacrylates altogether. Although many studies have used cyanoacrylates and report no ill effects, these glues are consistently more harmful to insects than alternatives. In particular, despite the results of Toppa et al. (2020) on the stingless bee *Melipona quadrifasciata* (le Peletier), to the author's knowledge there has been no proper test of the potential effect of cyanoacrylates on honeybees (*Apis mellifera*, L.) or bumble bees (*Bombus* spp.). Koenig and Petersen (2022) showed no significant effect of cyanoacrylates on the number of honeybees observed in experimental hives when compared to bees tagged with wood glue. However, there is no comparison of tagged bees to untagged bees or to glue-alone treatments, and the number of bees was visually assessed on live colonies containing many untagged individuals. While not an experimental paper, Scheiner et al. (2013) state that "super glue is not suitable because bees will die quickly" (note that 'super glue' colloquially refers to cyanoacrylate based glues) while discussing glueing honeybees to flight testing apparatus. Switzer and Combes (2016) found differences in the sonification frequency of paint marked bumblebees and bees which had a tag attached using cyanoacrylate. The author believes a more straightforward test of cyanoacrylates on honeybees and bumblebees should be carried out as a follow up to the work of Koenig and Petersen (2022), perhaps incorporating some of the techniques used by Toppa et al. (2020) to rule out the possibility of muscular damage.

Neither the custom-built Earwig Immobilisation Rings, nor the commercially produced bee marking cages could consistently immobilise earwigs. Given the variability in size and strength of individuals, a weight-based solution may not be ideal. Pope *et al.* (2013, 2015) used Blue-tack® putty (Bostik Ltd., Leicestershire, UK) to immobilise *Otiorhynchus sulcatus* (Fabricius; vine weevil).

The author believes Blue-tack® may be too firm to press earwigs into without harm, but a slightly softer putty may be a better method of immobilising earwigs than bee marking cages.

As stated at the start of this section, the automated tracking of earwigs in the field would be highly valuable. To date, no technology seems ideally suited to accomplishing this task. Passive RFID tags using a mobile antenna would appear to be one of the more promising possibilities, although currently the tags appropriate for such systems may be too large for use with earwigs. If a mesocosm approach is taken, then video monitoring should be considered for its potential trade-offs with RFID. Video monitoring under red light might be a suitable alternative, although the author is unaware of how red light affects the performance of tracking software. The video monitoring units created by Zantiks Ltd. (Cambridge, UK), or a similar technology, may be suitable. The use of an infra-red camera allows the experimental arenas to use materials opaque to visible light that are transparent to infra-red. In this way, areas of brightness and darkness can be created in the experimental arena and monitored with equal effectiveness by the software.

5.4. Grower recommendations

Although earwigs can cause some secondary damage to apples, the weight of evidence shows they are a net-beneficial in apple orchards. Unlike some beneficial insects, it may be difficult to tell if earwigs are having an effect in an orchard from daytime observations. And, if you have a WAA infestation, then releasing earwigs will not affect existing colonies a great deal. Instead, earwigs are likely most useful to prevent WAA outbreaks in the first place. Having a large population of earwigs in an orchard makes it more likely for WAA to be consumed before it becomes a noticeable issue. When trying to achieve high numbers of earwigs in an orchard, providing artificial shelters and bare earth in the row bed are advised. Tilling and spraying with harmful insecticides such as spinosad, indoxacarb, and deltamethrin, should both be avoided. Tilling will be most damaging from November to May, while insecticides will be most harmful from May to October. If augmentative releases are carried out to supplement these management practices, commit to carrying out releases for at least two years. Refuge traps are an effective way to gather earwigs for augmentative releases, and can be left after release to act as artificial shelters. Consider capturing earwigs from strawberries, raspberries, or cherries, where they can be damaging rather than beneficial.

5.5. Conclusions

Overall, there is a great deal that is still unknown about earwig and WAA biology and interactions in apple orchards. The variability in their abundance between different orchards needs further exploration, although the availability of shelter, and soil characteristics may be important factors for earwig populations. There was evidence for an effect of earwigs on WAA populations in the

orchards studied, without an augmentative release of earwigs. This effect appeared to be mediated by management practices, with more effective control of WAA by earwigs in conventionally compared to organically managed orchards. Radio frequency identification may not be an ideal for the remote monitoring of earwigs in the field in its current state, but it could be made easily applicable in mesocosm studies.

Key findings from this project are:

- Earwigs may be more beneficial in conventionally managed orchards rather than organic orchards
- Bare earth in apple orchards may benefit earwigs
- Moss and algae, known food sources for earwigs, were not associated with the presence of earwigs
- There was some direct molecular evidence for earwig consumption of WAA, but new primers need to be designed that are WAA specific
- Earwig presence did not differ between conventionally and organically managed orchards, WAA was more often present in organic orchards
- Artificial shelters in apple trees may lead to an increase in the abundance of earwigs in those same trees
- Cyanoacrylate based superglues appear toxic to earwigs, but less toxic alternatives are not effective
- Thermoplastic glue is likely the best compromise between toxicity and effectiveness when attaching tags to earwigs
- Data can be collected from RFID-tagged earwigs, but more work is needed to design effective mesocosms for the study of their behaviour

6. References

- Alins, G., Lordan, J., Rodríguez-Gasol, N., Arnó, J. and Peñalver-Cruz, A. (2023) 'Earwig releases provide accumulative biological control of the woolly apple aphid over the years', *Insects*, 14(11), pp. 890–890. Available at: <https://doi.org/10.3390/insects14110890>
- Alspach, P.A. and Bus, V.G.M. (1999) 'Spatial variation of woolly apple aphid (*Eriosoma lanigerum*, Hausmann) in a genetically diverse apple planting', *New Zealand Journal of Ecology*, 23(1), p. 6.
- Asante, S.K. (1995) 'Functional responses of the European earwig and two species of coccinellids to densities of *Eriosoma lanigerum* (Hausmann) (Hemiptera: Aphididae)', *Australian Journal of Entomology*, 34(2), pp. 105–109.
- Asante, S.K., Danthanarayana, W. and Cairns, S.C. (1993) 'Spatial and temporal distribution patterns of *Eriosoma lanigerum* (Homoptera: Aphididae) on apple', *Environmental Entomology*, 22(5), pp. 1060–1065. Available at: <https://doi.org/10.1093/ee/22.5.1060>
- Atwell, H.C. (1927) 'The European Earwig (*Forficula auricularia*, Linn.)', *19th Biennial report of the Oregon State Board of Horticulture*, pp. 86-103.
- Bangels, E., Alhmedi, A., Akkermans, W., Bylemans, D. and Belien, T. (2021) 'Towards a knowledge-based decision support system for integrated control of woolly apple aphid, *Eriosoma lanigerum*, with maximal biological suppression by the parasitoid *Aphelinus mali*', *Insects*, 12(6), p. 479. Available at: <https://doi.org/10.3390/insects12060479>
- Barbagallo, S., Cravedi, P., Pasqualini, E. and Patti, I. (1997) *Aphids of the principal fruit-bearing crops*. Milano: Bayer; Available at: <https://www.sidalc.net/search/Record/KOHA-OAI-AGRO:10714/Description> (Accessed: 10 March 2025)
- Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015) 'Fitting linear mixed-effects models using lme4', *Journal of Statistical Software*, 67(1), pp. 1–48. Available at: <https://doi.org/10.18637/jss.v067.i01>
- Beall, G. (1932) 'The life history and behavior of the European earwig, *Forficula auricularia*, L. in British Columbia', *Journal of the Entomological Society of British Columbia*, 29, pp. 28–44.
- Beers, E., Cockfield, S. and Fazio, G. (2007) 'Biology and management of woolly apple aphid, *Eriosoma lanigerum* (Hausmann), in Washington State', *Proceedings of the IOBC*, 30(4), pp. 37–42.
- Beers, E.H., Horton, D.R. and Miliczky, E. (2016) 'Pesticides used against *Cydia pomonella* disrupt biological control of secondary pests of apple', *Biological Control*, 102, pp. 35–43. Available at: <https://doi.org/10.1016/j.biocontrol.2016.05.009>
- Beliën, T., Bangels, E., Peusens, G., Goossens, D., Berkvens, N. and Viaene, N. (2010) 'Towards improved control of woolly apple aphid (*Eriosoma lanigerum*) in integrated fruit production',

- Acta Horticulturae*, (917), pp. 15–22. Available at:
<https://doi.org/10.17660/actahortic.2011.917.1>
- Bergh, J.C. and Stallings, J.W. (2016) 'Field evaluations of the contribution of predators and the parasitoid, *Aphelinus mali*, to biological control of woolly apple aphid, *Eriosoma lanigerum*, in Virginia, USA', *BioControl*, 61(2), pp. 155–165. Available at:
<https://doi.org/10.1007/s10526-016-9714-7>
- Biello, R., Singh, A., Godfrey, C.J., Fernández, F.F., Mugford, S.T., Powell, G., Hogenhout, S.A. and Mathers, T.C. (2021) 'A chromosome-level genome assembly of the woolly apple aphid, *Eriosoma lanigerum* Hausmann (Hemiptera: Aphididae)', *Molecular Ecology Resources*, 21(1), pp. 316–326. Available at: <https://doi.org/10.1111/1755-0998.13258>
- Binns, M., Hoffmann, A.A., Helden, M. van, Heddle, T., Hill, M.P., Macfadyen, S., Nash, M.A. and Umina, P.A. (2021) 'Lifecycle of the invasive omnivore, *Forficula auricularia*, in Australian grain growing environments', *Pest Management Science*, 77(4), pp. 1818–1828. Available at: <https://doi.org/10.1002/ps.6206>
- Binns, M.R., Macfadyen, S. and Umina, P.A. (2022) 'The dual role of earwigs (Dermaptera) in winter grain crops in Australia', *Journal of Applied Entomology*, 146(3), pp. 272–283. Available at: <https://doi.org/10.1111/jen.12959>
- Bischoff, R., Pokharel, P., Miedtke, P., Piepho, H.-P. and Petschenka, G. (2024) 'Environmental complexity and predator density mediate a stable earwig-woolly apple aphid interaction', *Basic and applied ecology*, 74, pp. 108–114. Available at:
<https://doi.org/10.1016/j.baae.2023.12.003>
- Blackman, R.L. and Eastop, V.F. (1984) *Aphids on the World's Crops. An identification and information guide*. Chichester: John Wiley & Sons Ltd. Available at:
<https://www.cabidigitallibrary.org/doi/full/10.5555/19860532764> (Accessed: 10 March 2025)
- Boiteau, G., Meloche, F., Vincent, C. and Leskey, T.C. (2009) 'Effectiveness of glues used for harmonic radar tag attachment and impact on survival and behavior of three insect pests', *Environmental Entomology*, 38(1), pp. 168–175. Available at:
<https://doi.org/10.1603/022.038.0121>
- Boiteau, G., Vincent, C., Meloche, F. and Leskey, T.C. (2010) 'Harmonic radar: assessing the impact of tag weight on walking activity of Colorado potato beetle, *Plum curculio*, and Western corn rootworm', *Journal of Economic Entomology*, 103(1), pp. 63–69. Available at:
<https://doi.org/10.1603/ec09113>
- Bureau de Roince, C., Lavigne, C., Ricard, J.-M., Franck, P., Bouvier, J.-C., Garcin, A. and Symondson, W.O.C. (2012) 'Predation by generalist predators on the codling moth versus a closely-related emerging pest the oriental fruit moth: a molecular analysis', *Agricultural and Forest Entomology*, 14(3), pp. 260–269. Available at: <https://doi.org/10.1111/j.1461-9563.2011.00564.x>

- Breheny, P. and Burchett, W. (2017) 'Visualization of regression models using visreg', *The R Journal*, 9(2), p. 56. Available at: <https://doi.org/10.32614/rj-2017-046>
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M. and Bolker, B.M. (2017) 'glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling', *The R Journal*, 9(2), p. 378. Available at: <https://doi.org/10.32614/rj-2017-066>
- Brown, M.W., Schmitt, J.J., Ranger, S. and Hogmire, H.W. (1995) 'Yield reduction in apple by edaphic woolly apple aphid (Homoptera: Aphididae) populations', *Journal of Economic Entomology*, 88(1), pp. 127–133. Available at: <https://doi.org/10.1093/jee/88.1.127>
- Bulgarini, G., Badra, Z., Leonardi, S. and Maistrello, L. (2020) 'Predatory ability of generalist predators on eggs, young nymphs and adults of the invasive *Halyomorpha halys* in southern Europe', *BioControl*, 66(3), pp. 355–366. Available at: <https://doi.org/10.1007/s10526-020-10066-3>
- Burnip, G.M., Daly, J.M., Hackett, J.K. and Suckling, D.M. (2002) 'European earwig phenology and effect of understorey management on population estimation', *Proceedings of the New Zealand Weed Control Conference*, 55, pp. 390–395. Available at: <https://doi.org/10.30843/nzpp.2002.55.3938>
- Buzzetti, F.M., Carotti, G., Fontana, P. and Tirello, P. (2003) 'Observations on the flight of Dermaptera and on an extraordinary flight of the common Earwig *Forficula auricularia* observed in Sardinia (Dermaptera Forficulidae)', *Bollettino della Società Entomologica Italiana*, 135(2), pp. 67–70. Available at: https://www.researchgate.net/profile/Paolo-Fontana-3/publication/257234082_Observations_on_the_flight_of_Dermaptera_and_on_an_extraordinary_flight_of_the_common_Earwig_Foricula_auricularia_observed_in_Sardinia_Dermaptera_Foriculidae/links/61e686325779d35951b84409/Observations-on-the-flight-of-Dermaptera-and-on-an-extraordinary-flight-of-the-common-Earwig-Forficula-auricularia-observed-in-Sardinia-Dermaptera-Forficulidae.pdf
- Carroll, D.P., Walker, J.T.S. and Hoyt, S.C. (1985) 'European Earwigs (Dermaptera: Forficulidae) fail to control apple aphids on bearing apple trees and woolly apple aphids (Homoptera: Aphididae) in apple rootstock stool beds', *Journal of Economic Entomology*, 78(4), pp. 972–974. Available at: <https://doi.org/10.1093/jee/78.4.972>
- Childs, L. (1929) 'The relation of woolly apple aphid to perennial canker infection with other notes on the disease', *State Library of Oregon Digital Collections*, Available at: <https://digitalcollections.library.oregon.gov/nodes/view/189614> (Accessed: 18 October 2024)

- Cisneros, J., Goulson, D., Derwent, L.C., Penagos, D.I., Hernández, O. and Williams, T. (2002) 'Toxic effects of spinosad on predatory insects', *Biological Control*, 23(2), pp. 156–163. Available at: <https://doi.org/10.1006/bcon.2001.1000>
- Cossins, A.R. and Bowler, K. (1987) *Temperature biology of animals*. London: Chapman And Hall.
- Cross, J., Berrie, A., Johnson, J., Biddlecombe, T., Pennell, D., Luton, L. and Ashdown, C. (n.d.) 'Apple Best Practice Guide - Pest and Disease Control' NIAB. Available at: <https://www.niab.com/membership/niab-fruit/apple-best-practice-guide/apple-best-practice-guide-pest-and-disease-control> (Accessed: 4 December 2024)
- Crumb, S.E., Bonn, A.E. and Eide, P.M. (1941) *The European earwig*. Technical bulletin number 766. Washington: United States Department of Agriculture. Available at: https://books.google.com/books?hl=en&lr=&id=zYaLevC_th4C&oi=fnd&pg=PA3&dq=Crumb+SE,+Eide+PM,+Bonn+AE,+1941.+The+European+Earwig.+Technical+Bulletin.+United+States+Department+of+Agriculture,+766.+Washington,+D.C.,+76+pp.&ots=NbDwoCUii5&sig=NR9_eHusbRHghDQQF-Ur1klwArU (Accessed: 20 November 2024)
- Dag, O., Dolgun, A. and Konar, N. (2018) 'onewaytests: an R package for one-way tests in independent groups designs', *The R Journal*, 10(1), p. 175. Available at: <https://doi.org/10.32614/rj-2018-022>
- Debras, J.-F., Dussaud, A., Rieux, R. and Dutoit, T. (2007) 'Recherche prospective sur le rôle "source" des haies en production fruitière intégrée. Le cas des perce-oreilles : *Forficula auricularia* L. et *Forficula pubescens* Gené', *Comptes Rendus. Biologies*, 330(9), pp. 664–673. Available at: <https://doi.org/10.1016/j.crvi.2007.07.003>
- Dedryver, C.-A., Le Ralec, A. and Fabre, F. (2010) 'The conflicting relationships between aphids and men: a review of aphid damage and control strategies', *Comptes Rendus Biologies*, 333(6), pp. 539–553. Available at: <https://doi.org/10.1016/j.crvi.2010.03.009>
- Dib, H., Jamont, M., Sauphanor, B. and Capowiez, Y. (2016a) 'Individual and combined effects of the generalist *Forficula auricularia* and the specialist *Episyrphus balteatus* on *Dysaphis plantaginea* – are two predators better than one?', *Entomologia Experimentalis et Applicata*, 161(1), pp. 1–10. Available at: <https://doi.org/10.1111/eea.12484>
- Dib, H., Jamont, M., Sauphanor, B. and Capowiez, Y. (2016b) 'The feasibility and efficacy of early-season releases of a generalist predator (*Forficula auricularia* L.) to control populations of the RAA (*Dysaphis plantaginea* Passerini) in Southeastern France', *Bulletin of Entomological Research*, 106(2), pp. 233–241. Available at: <https://doi.org/10.1017/S0007485315001042>
- Dib, H., Siegwart, M., Delattre, T., Perrin, M. and Lavigne, C. (2020) 'Does combining *Forficula auricularia* L. (Dermaptera: Forficulidae) with *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) enhance predation of rosy apple aphid, *Dysaphis plantaginea* Passerini

- (Hemiptera: Aphididae)?', *Biological Control*, 151, pp. 104394–104394. Available at: <https://doi.org/10.1016/j.biocontrol.2020.104394>
- Dobler, R. and Kölliker, M. (2010) 'Kin-selected siblicide and cannibalism in the European earwig', *Behavioral Ecology*, 21(2), pp. 257–263. Available at: <https://doi.org/10.1093/beheco/arp184>
- Dobler, R. and Kölliker, M. (2011) 'Influence of weight asymmetry and kinship on siblicidal and cannibalistic behaviour in earwigs', *Animal Behaviour*, 82(4), pp. 667–672. Available at: <https://doi.org/10.1016/j.anbehav.2011.06.017>
- Evans, K. and Longépé, V. (1996) 'The European earwig: getting the best of both worlds?' *The 2nd International Conference on Insect Pests in the Urban Environment*. Edinburgh, UK: Heriot Watt University. Available at: <https://www.icup.org.uk/media/nbwjf5m5/icup721.pdf>
- Ffrench-Constant, R.H. and Vickerman, G.P. (1985) 'Soil contact toxicity of insecticides to the European earwig *Forficula auricularia* [Dermaptera]', *Entomophaga*, 30(3), pp. 271–278. Available at: <https://doi.org/10.1007/BF02372228>
- Fountain, M.T. and Harris, A.L. (2015) 'Non-target consequences of insecticides used in apple and pear orchards on *Forficula auricularia* L. (Dermaptera: Forficulidae)', *Biological Control*, 91, pp. 27–33. Available at: <https://doi.org/10.1016/j.biocontrol.2015.07.007>
- Fox, J. and Weisberg, S. (2019) *An R companion to applied regression*. 3rd edn. Thousand Oaks, California: Sage Publications, Inc.
- Gobin, B., Marien, A., Davis, S. and Leirs, H. (2006) 'Enhancing earwig populations in Belgian orchards', *Communications in Agricultural and Applied Biological Sciences*, 71(2b), pp. 269–274.
- Gobin, B., Peusens, G., Moerkens, R. and Leirs, H. (2008b) 'Understanding earwig phenology in top fruit orchards', *Ecofruit-13th International Conference on Cultivation Technique and Phytopathological Problems in Organic Fruit-Growing*. Conference at Weinsberg (Germany), 18-20 February 2008. pp. 208–212. Available at: <http://orgprints.org/13678/>
- Godfrey, C.J. (2024) *Resistance and susceptibility in interactions between apple and woolly aphid*. PhD Thesis. Harper Adams University. Available at: <https://hau.repository.guildhe.ac.uk/id/eprint/18141/> (Accessed: 12 March 2025)
- Gontijo, L.M., Beers, E.H. and Snyder, W.E. (2015) 'Complementary suppression of aphids by predators and parasitoids', *Biological Control*, 90, pp. 83–91. Available at: <https://doi.org/10.1016/j.biocontrol.2015.06.002>
- González Miguéns, R., Nozal, E., Jiménez Ruiz, Y., Mas-Peinado, P., Ghanavi, H. and García-París, M. (2020) 'Speciation patterns in the *Forficula auricularia* species complex: cryptic and not so cryptic taxa across the western Palaearctic region', 190(3), pp. 788–823. Available at: <https://doi.org/10.1093/zoolinnean/zlaa070>

- Goossens, D., Bangels, E., Belien, T., Schoevaerts, C. and De Maeyer, L. (2011) 'Optimal profit of the parasitism by *Aphelinus mali* in an IPM complementary strategy for the control of *Eriosoma lanigerum*', *Communications in agricultural and applied biological sciences*, 76(3), pp. 457–465.
- Greenstone, M.H., Rowley, D.L., Weber, D.C., Payton, M.E. and Hawthorne, D.J. (2007) 'Feeding mode and prey detectability half-lives in molecular gut-content analysis: an example with two predators of the Colorado potato beetle', *Bulletin of Entomological Research*, 97(2), pp. 201–209. Available at: <https://doi.org/10.1017/s000748530700497x>
- Guerrieri, E. and Digilio, M.C. (2008) 'Aphid-plant interactions: a review', *Journal of Plant Interactions*, 3(4), pp. 223–232. Available at: <https://doi.org/10.1080/17429140802567173>
- Guillet, S., Guiller, A., Deunff, J. and Vancassel, M. (2000) 'Analysis of a contact zone in the *Forficula auricularia* L. (Dermaptera: Forficulidae) species complex in the Pyrenean Mountains', *Heredity*, 85(5), pp. 444–449. Available at: <https://doi.org/10.1046/j.1365-2540.2000.00775.x>
- Hanel, A., Nottingham, L.B., Orpet, R.J., Hilton, R., Northfield, T.D. and Schmidt-Jeffris, R. (2025) 'Evaluating trapping methods to increase earwig capture in temperate tree fruit crops', *Journal of Economic Entomology*, p. toaf018. Available at: <https://doi.org/10.1093/jee/toaf018>
- Hanel, A., Orpet, R.J., Hilton, R., Nottingham, L., Northfield, T.D. and Schmidt-Jeffris, R. (2023) 'Turning a pest into a natural enemy: removing earwigs from stone fruit and releasing them in pome fruit enhances pest control', *Insects*, 14(12), pp. 906–906. Available at: <https://doi.org/10.3390/insects14120906>
- Happe, A.-K., Roquer-Beni, L., Bosch, J., Alins, G. and Mody, K. (2018) 'Earwigs and woolly apple aphids in integrated and organic apple orchards: responses of a generalist predator and a pest prey to local and landscape factors', *Agriculture, Ecosystems & Environment*, 268, pp. 44–51. Available at: <https://doi.org/10.1016/j.agee.2018.09.004>
- He, X.Z., Wang, Q. and Xu, J. (2008) 'European earwig as a potential biological control agent of apple leafcurling midge', *New Zealand Plant Protection*, 61, pp. 343–349. Available at: <https://doi.org/10.30843/nzpp.2008.61.6814>
- Helsen, H., Trapman, M., Polfliet, M. and Simonse, J. (2007) 'Presence of the common earwig *Forficula auricularia* L. in apple orchards and its impact on the woolly apple aphid *Eriosoma lanigerum* (Hausmann)'. *IOBC Wprs Bulletin*, 30(4), pp. 31–35. Available at: https://www.researchgate.net/publication/46385685_Presence_of_the_common_earwig_Fo_rficula_auricularia_L_in_apple_orchards_and_its_impact_on_the_woolly_apple_aphid_Erio_soma_lanigerum_Hausmann

- Heunis, J.M. and Pringle, K.L. (2003) 'The susceptibility of *Aphelinus mali* (Haldeman), a parasitoid of *Eriosoma lanigerum* (Hausmann), to pesticides used in apple orchards in the Elgin area, Western Cape Province, South Africa', *African entomology*, 11(1), pp. 91–95.
- Hill, M.R., Binns, M.M., Umina, P.A., Hoffmann, A.A. and Macfadyen, S. (2019) 'Climate, human influence and the distribution limits of the invasive European earwig, *Forficula auricularia*, in Australia', *Pest Management Science*, 75(1), pp. 134–143. Available at: <https://doi.org/10.1002/ps.5192>
- Holý, K. and Stará, J. (2020) 'Laboratory evaluation of the effect of insecticides on *Chrysoperla carnea* (Neuroptera: Chrysopidae), *Forficula auricularia* (Dermaptera: Forficulidae), *Adalia bipunctata* (Coleoptera: Coccinellidae) and *Harmonia axyridis* (Coleoptera: Coccinellidae)', *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis*, 68(3), pp. 497–506. Available at: <https://doi.org/10.11118/actaun202068030497>
- Jana, N., Michal, S., Jana, O. and Radek, M. (2021) '*Forficula auricularia* (Dermaptera) in orchards: monitoring seasonal activity, the effect of pesticides, and the perception of European fruit growers on its role as a predator or pest', *Pest Management Science*, 77(4), pp. 1694–1704. Available at: <https://doi.org/10.1002/ps.6189>
- Kassambara, A. (2023) 'rstatix: pipe-friendly framework for basic statistical tests', R package version 0.7.2. Available at: <https://rpkgs.datanovia.com/rstatix/>
- Kirkpatrick, D.M., Rice, K.B., Ibrahim, A., Morrison, W.R. and Leskey, T.C. (2019) 'Influence of harmonic radar tag attachment on nymphal *Halyomorpha halys* mobility, survivorship, and detectability', *Entomologia Experimentalis et Applicata*, 167(12), pp. 1020–1029. Available at: <https://doi.org/10.1111/eea.12861>
- Kocarek, P. (1998) 'Life cycles and habitat associations of three earwig (Dermaptera) species in lowland forest and its surroundings', *Biologia*, 53, pp. 205–211.
- Koenig, P.A. and Petersen, K.H. (2022) 'Best practices for instrumenting honey bees', *Scientific Reports*, 12(1), p. 12796. Available at: <https://doi.org/10.1038/s41598-022-16168-5>
- Kuznetsova, A., Brockhoff, P.B. and Christensen, R.H.B. (2017) 'LmerTest package: tests in linear mixed effects models', *Journal of Statistical Software*, 82(13), pp. 1–26. Available at: <https://doi.org/10.18637/jss.v082.i13>
- Lamb, R.J. (1974) *Earwig travel in relation to habitat*. PhD Thesis. University of British Columbia. Available at: <https://open.library.ubc.ca/soa/cIRcle/collections/ubctheses/831/items/1.0100004> (Accessed: 3 December 2024)
- Lamb, R.J. (1975) 'Effects of dispersion, travel, and environmental heterogeneity on populations of the earwig *Forficula auricularia* L.', *Canadian Journal of Zoology*, 53(12), pp. 1855–1867. Available at: <https://doi.org/10.1139/z75-219>

- Lamb, R.J. and Wellington, W.G. (1975) 'Life history and population characteristics of the European earwig, *Forficula auricularia* (Dermaptera: Forficulidae), at Vancouver, British Columbia', *The Canadian Entomologist*, 107(8), pp. 819–824. Available at: <https://doi.org/10.4039/Ent107819-8>
- Landt, J. (2005) 'The history of RFID', *IEEE Potentials*, 24(4), pp. 8–11. Available at: <https://doi.org/10.1109/mp.2005.1549751>
- Le Navenant, A., Brouchoud, C., Capowiez, Y., Rault, M. and Suchail, S. (2021) 'How lasting are the effects of pesticides on earwigs? A study based on energy metabolism, body weight and morphometry in two generations of *Forficula auricularia* from apple orchards', *Science of The Total Environment*, 758, p. 143604. Available at: <https://doi.org/10.1016/j.scitotenv.2020.143604>
- Le Navenant, A., Siegwart, M., Maugin, S., Capowiez, Y. and Rault, M. (2019) 'Metabolic mechanisms and acetylcholinesterase sensitivity involved in tolerance to chlorpyrifos-ethyl in the earwig *Forficula auricularia*', *Chemosphere*, 227, pp. 416–424. Available at: <https://doi.org/10.1016/j.chemosphere.2019.04.065>
- Leisch, F., Weingessel, A. and Hornik, K. (2024) 'bindata: generation of artificial binary data', R package version 0.9-22. Available at: <https://doi.org/10.32614/CRAN.package.bindata>
- Lenth, R. (2025) 'emmeans: estimated marginal means, aka least-squares means', R package version 1.10.7-100003. Available at: <https://rvlenth.github.io/emmeans/>
- Logan, D.P., Maher, B.J. and Connolly, P.G. (2011) 'Increased numbers of earwigs (*Forficula auricularia*) in kiwifruit orchards are associated with fewer broadspectrum sprays', *New Zealand Plant Protection*, 64, pp. 49–54. Available at: <https://doi.org/10.30843/nzpp.2011.64.5955>
- Logan, D.P., Maher, B.J. and Rowe, C.A. (2017) 'Predation of diaspidid scale insects on kiwifruit vines by European earwigs, *Forficula auricularia*, and steel-blue ladybirds, *Halmus chalybeus*', *BioControl*, 62(4), pp. 469–479. Available at: <https://doi.org/10.1007/s10526-017-9797-9>
- Logan, D.P., Maher, B.J., Connolly, P.G. and Pettigrew, M.J. (2007) 'Effect of cardboard shelter traps on predation of diaspidid scale insects by European earwigs *Forficula auricularia* in kiwifruit', *New Zealand Plant Protection*, 60, pp. 241–248. Available at: <https://doi.org/10.30843/nzpp.2007.60.4617>
- Maczey, N., Edgington, S., Moore, D., and Haye, T. (2016) 'Biology and host range testing of *Triarthria setipennis* and *Ocytata pallipes* (Diptera: Tachinidae) for the control of the European earwig (*Forficula auricularia*)', *Biocontrol Science and Technology*, 26(4), pp. 447–461. Available at: <https://doi.org/10.1080/09583157.2015.1123675>

- Maher, B.J., Logan, D.P. and Connolly, P.G. (2006) 'Effect of mineral oil and diazinon residues on the predator European earwig *Forficula auricularia* in kiwifruit', *New Zealand Plant Protection*, 59, pp. 202–207. Available at: <https://doi.org/10.30843/nzpp.2006.59.4542>
- Malagnoux, L., Capowiez, Y. and Rault, M. (2015) 'Impact of insecticide exposure on the predation activity of the European earwig *Forficula auricularia*', *Environmental Science and Pollution Research*, 22(18), pp. 14116–14126. Available at: <https://doi.org/10.1007/s11356-015-4520-9>
- Malagnoux, L., Marliac, G., Simon, S., Rault, M. and Capowiez, Y. (2015) 'Management strategies in apple orchards influence earwig community', *Chemosphere*, 124, pp. 156–162. Available at: <https://doi.org/10.1016/j.chemosphere.2014.12.024>
- Markó, V., Blommers, L.H.M., Bogya, S., and Helsen, H. (2008) 'Kaolin particle films suppress many apple pests, disrupt natural enemies and promote woolly apple aphid', *Journal of Applied Entomology*, 132(1), pp. 26–35. Available at: <https://doi.org/10.1111/j.1439-0418.2007.01233.x>
- Marshall, A.T. and Beers, E.H. (2021) 'Efficacy and nontarget effects of net exclusion enclosures on apple pest management', *Journal of Economic Entomology*, 114(4), pp. 1681–1689. Available at: <https://doi.org/10.1093/jee/toab094>
- Marshall, A.T. and Beers, E.H. (2022) 'Exclusion netting affects apple arthropod communities', *Biological Control*, 165, p. 104805. Available at: <https://doi.org/10.1016/j.biocontrol.2021.104805>
- McKerchar, M., Potts, S.G., Fountain, M.T., Garratt, M.P.D. and Westbury, D.B. (2020) 'The potential for wildflower interventions to enhance natural enemies and pollinators in commercial apple orchards is limited by other management practices', *Agriculture, Ecosystems & Environment*, 301, p. 107034. Available at: <https://doi.org/10.1016/j.agee.2020.107034>
- Meier, U., Graf, H., Hack, H., Hess, M., Kennel, W., Klose, R., Mappes, D., Seipp, D., Stauss, R., Streif, J. and Boom, T. (1994) 'Phänologische Entwicklungsstadien des Kernobstes (*Malus domestica* Borkh. und *Pyrus communis* L.), des Steinobstes (*Prunus*-Arten), der Johannisbeere (*Ribes*-Arten) und der Erdbeere (*Fragaria x ananassa* Duch.).', *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes*, 46(7), pp. 141–153. Available at: <https://agris.fao.org/search/en/providers/123819/records/647362a3e17b74d22253c468>
- Merleau, L.-A., Larrigaldie, I., Bousquet, O., Devers, S., Keller, M., Lécureuil, C., and Meunier, J. (2022) 'Exposure to pyriproxyfen (juvenile hormone agonist) does not alter maternal care and reproduction in the European earwig', *Environmental Science and Pollution Research*, 29(48), pp. 72729–72746. Available at: <https://doi.org/10.1007/s11356-022-20970-z>
- Meunier, J., Dufour, J., Van Meyel, S., Rault, M. and Lécureuil, C. (2020) 'Sublethal exposure to deltamethrin impairs maternal egg care in the European earwig *Forficula*

- auricularia*', *Chemosphere*, 258, p. 127383. Available at:
<https://doi.org/10.1016/j.chemosphere.2020.127383>
- Moerkens, R., Leirs, H., Peusens, G. and Gobin, B. (2009) 'Are populations of European earwigs, *Forficula auricularia*, density dependent?', *Entomologia Experimentalis et Applicata*, 130(2), pp. 198–206. Available at: <https://doi.org/10.1111/j.1570-7458.2008.00808.x>
- Moerkens, R., Leirs, H., Peusens, G. and Gobin, B. (2010) 'Dispersal of single- and double-brood populations of the European earwig, *Forficula auricularia*: a mark-recapture experiment, *Entomologia Experimentalis et Applicata*, 137(1), pp. 19–27. Available at:
<https://doi.org/10.1111/j.1570-7458.2010.01031.x>
- Moerkens, R., Leirs, H., Peusens, G., Beliën, T. and Gobin, B. (2012) 'Natural and human causes of earwig mortality during winter: temperature, parasitoids and soil tillage', *Journal of Applied Entomology*, 136(7), pp. 490–500. Available at: <https://doi.org/10.1111/j.1439-0418.2011.01676.x>
- Mueller, T.F., Blommers, L.H.M. and Mols, P.J.M. (1988) 'Earwig (*Forficula auricularia*) predation on the woolly apple aphid, *Eriosoma lanigerum*', *Entomologia Experimentalis et Applicata*, 47(2), pp. 145–152. Available at: <https://doi.org/10.1111/j.1570-7458.1988.tb01129.x>
- Nauen, R., Reckmann, U., Thomzik, J. and Thielert, W. (2007) 'Biological profile of spirotetramat (Movento)—a new two way systemic (amimobile) insecticide against sucking pests', *Bayer Crop Science Journal*, 61(2), pp. 245–278. Available at:
https://www.researchgate.net/publication/267198550_Biological_profile_of_spirotetramat_Movento-a_new_two_way_systemic_amimobile_insecticide_against_sucking_pests
- Ngai, E.W.T., Moon, K.K.L., Riggins, F.J. and Yi, C.Y. (2008) 'RFID research: an academic literature review (1995–2005) and future research directions', *International Journal of Production Economics*, 112(2), pp. 510–520. Available at:
<https://doi.org/10.1016/j.ijpe.2007.05.004>
- Nicholas, A. and Thwaite, W. (2003) 'Toxicity of chemicals commonly used in Australian apple orchards to the European earwig '*Forficula auricularia*' L. (Dermaptera: Forficulidae)', *General and Applied Entomology: The Journal of the Entomological Society of New South Wales*, 32, pp. 9–12 Available at:
<https://www.entsoicnsw.org.au/images/stories/media/nicholas%20and%20thwaite.pdf>
- Nicholas, A., Thwaite, W. and Spooner-Hart, R. (1999) 'Arthropod abundance in an Australian apple orchard under mating disruption and supplementary insecticide treatments for codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae)', *Australian Journal of Entomology*, 38(1), pp. 23–29. Available at: <https://doi.org/10.1046/j.1440-6055.1999.00073.x>
- Nicholas, A.H., Spooner-Hart, R.N. and Vickers, R.A. (2005) 'Abundance and natural control of the woolly aphid *Eriosoma lanigerum* in an Australian apple orchard IPM program', *BioControl*, 50(2), pp. 271–291. Available at: <https://doi.org/10.1007/s10526-004-0334-2>

- Nogueira, R.M., Bragança, G.P.P., Picoli, E.A.T., de Oliveira, D.C. and Isaias, R.M.D.S. (2025) 'Phloem cell responses to the feeding activity of *Eriosoma lanigerum* on *Malus domestica*', *Frontiers in Plant Science*, 16, p. 1507552. Available at: <https://doi.org/10.3389/fpls.2025.1507552>
- Nogueira, R.M., Freitas, M.S.C., Picoli, E.A.T. and Isaias, R.M.D.S. (2024) 'Implications of cell wall immunocytochemical profiles on the structural and functional traits of root and stem galls induced by *Eriosoma lanigerum* on *Malus domestica*', *Protoplasma*, 261(5), pp. 911–926. Available at: <https://doi.org/10.1007/s00709-024-01939-w>
- O'Rourke, D. (2021) 'Economic importance of the world apple industry', in S.S. Korban (ed.) *The Apple Genome*. Cham: Springer International Publishing, pp. 1–18. Available at: https://doi.org/10.1007/978-3-030-74682-7_1
- Ogle, D.H., Doll, J.C., Wheeler, A.P. and Dinno, A. (2025) 'FSA: simple fisheries stock assessment methods', R package version 0.9.6. Available at: <https://CRAN.R-project.org/package=FSA>
- Orpet, R.J., Crowder, D.W. and Jones, V.P. (2019a) 'Woolly apple aphid generalist predator feeding behavior assessed through video observation in an apple orchard', *Journal of Insect Behavior*, 32(2), pp. 153–163. Available at: <https://doi.org/10.1007/s10905-019-09722-z>
- Orpet, R.J., Crowder, D.W. and Jones, V.P. (2019b) 'Biology and management of European earwig in orchards and vineyards', *Journal of Integrated Pest Management*, 10(1), pp. 1–9. Available at: <https://doi.org/10.1093/jipm/pmz019>
- Orpet, R.J., Goldberger, J.R., Crowder, D.W. and Jones, V.P. (2019a) 'Field evidence and grower perceptions on the roles of an omnivore, European earwig, in apple orchards', *Biological Control*, 132, pp. 189–198. Available at: <https://doi.org/10.1016/j.biocontrol.2019.02.011>
- Orpet, R.J., Jones, V.P., Reganold, J.P. and Crowder, D.W. (2019b) 'Effects of restricting movement between root and canopy populations of woolly apple aphid', *PLOS ONE*, 14(5), p. e0216424. Available at: <https://doi.org/10.1371/journal.pone.0216424>
- Pavón-Gozalo, P., Mila, B., Aleixandre, P., Calderón, J., Zaldívar-riverón, A., Hernández-Montoya, J.C. and García-París, M. (2011) 'Invasion of two widely separated areas of Mexico by *Forficula auricularia* (Dermaptera: Forficulidae)', *The Florida Entomologist*, 94, pp. 1088–1090. Available at: <https://doi.org/10.2307/23065878>
- Peusens, G. and Gobin, B. (2008) 'Side effects of pesticides on the European earwig *Forficula auricularia* L. (Dermaptera: Forficulidae)', *IOBC Working Group "Pesticides and Beneficial Organisms"*. Conference at Berlin (Germany), 10-12 October 2007. 35, pp. 40-43. Available at: http://www.iobc-wprs.org/pub/bulletins/bulletin_2008_35_table_of_contents_abstracts.pdf
- Peusens, G., Beliën, T. and Gobin, B. (2010) 'Comparing different test methods for evaluating lethal side effects of some insecticides on the European earwig *Forficula auricularia* L.', *IOBC Working Group "Pesticides and Beneficial Organisms"*. Conference at Dubrovnik

- (Croatia), 7-9 October 2009. 55, pp. 95-100. Available at: <https://iobc-wprs.org/product/iobc-wprs-bulletin-vol-55-2010/>
- Peusens, G., Moerkens, R., Beliën, T. and Gobin, B. (2009) 'Side effects of plant protection products and biological interactions on the European earwig *Forficula auricularia* L.', *Communications in agricultural and applied biological sciences*, 74(2), pp. 411–417.
- Phillips, M.L. (1981) *The ecology of the common earwig Forficula auricularia in apple orchards*. PhD Thesis. University of Bristol. Available at: <https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.528387> (Accessed: 3 November 2020)
- Pike, N., Richard, D., Foster, W. and Mahadevan, L. (2002) 'How aphids lose their marbles', *Proceedings of the Royal Society B Biological Sciences*, 269(1497), pp. 1211–1215. Available at: <https://doi.org/10.1098/rspb.2002.1999>
- Piñol, J., Espadaler, X., Cañellas, N. and Pérez, N. (2009) 'Effects of the concurrent exclusion of ants and earwigs on aphid abundance in an organic citrus grove', *BioControl*, 54(4), pp. 515–527. Available at: <https://doi.org/10.1007/s10526-008-9203-8>
- Pope, T., Gundalai, E., Elliott, L., Blackshaw, R., Hough, G., Wood, A., Bennison, J., Prince, G. and Chandler, D. (2015) 'Recording the movement of adult vine weevil within strawberry crops using radio frequency identification tags', *Journal of Berry Research*, 5(4), pp. 197–206. Available at: <https://doi.org/10.3233/jbr-150102>
- Pope, T., Gundalai, E., Hough, G., Wood, A., Bennison, J., Prince, G. and Chandler, D. (2013) 'How far does a weevil walk?' *Aspects of Applied Biology*, 119, pp. 97–103.
- Quarrell, S.R., Arabi, J., Suwalski, A., Veuille, M., Wirth, T. and Allen, G.R. (2018) 'The invasion biology of the invasive earwig, *Forficula auricularia* in Australasian ecosystems', 20(6), pp. 1553–1565. Available at: <https://doi.org/10.1007/s10530-017-1646-3>
- Quarrell, S.R., Corkrey, R. and Allen, G.R. (2017) 'Predictive thresholds for forecasting the compatibility of *Forficula auricularia* and *Aphelinus mali* as biological control agents against woolly apple aphid in apple orchards', *BioControl*, 62(2), pp. 243–256. Available at: <https://doi.org/10.1007/s10526-017-9792-1>
- Ridley, L., Parrish, G., Chantry, T., Richmond, A., MacArthur, R. and Garthwaite, D. (2024). 'Orchards in the UK 2022 (Pesticide Usage Survey Report No. 311)'. *Fera Science Limited, Land Use & Sustainability Team*. Available at: <https://pusstats.fera.co.uk/home>
- Romeu-Dalmau, C., Espadaler, X. and Piñol, J. (2012) 'Abundance, interannual variation and potential pest predator role of two co-occurring earwig species in citrus canopies', *Journal of Applied Entomology*, 136(7), pp. 501–509. Available at: <https://doi.org/10.1111/j.1439-0418.2011.01671.x>
- Romeu-Dalmau, C., Espadaler, X. and Piñol, J. (2016) 'Management implications of earwigs' overwintering sites in a Mediterranean citrus grove', *International Journal of Pest*

- Management*, 62(2), pp. 129–134. Available at:
<https://doi.org/10.1080/09670874.2015.1129079>
- Romeu-Dalmau, C., Piñol, J. and Agustí, N. (2012) 'Detecting aphid predation by earwigs in organic citrus orchards using molecular markers', *Bulletin of Entomological Research*, 102(5), pp. 566–572. Available at: <https://doi.org/10.1017/s0007485312000132>
- Romeu-Dalmau, C., Piñol, J. and Espadaler, X. (2012) 'Friend or foe? The relative role of earwigs as pests versus biocontrol agents in citrus canopies', *Biological Control*, 63(2), pp. 143–149. Available at: <https://doi.org/10.1016/j.biocontrol.2012.06.010>
- Schauberger, P. and Walker, A. (2025) 'openxlsx: read, write and edit xlsx files' R package version 4.2.8. Available at: <https://github.com/ycphs/openxlsx>
- Scheiner, R., Abramson, C.I., Brodschneider, R., Crailsheim, K., Farina, W.M., Fuchs, S., Grünewald, B., Hahshold, S., Karrer, M., Koeniger, G., Koeniger, N., Menzel, R., Mujagic, S., Radspieler, G., Schmickl, T., Schneider, C., Siegel, A.J., Szopek, M. and Thenius, R. (2013) 'Standard methods for behavioural studies of *Apis mellifera*', *Journal of Apicultural Research*, 52(4), pp. 1–58. Available at: <https://doi.org/10.3896/IBRA.1.52.4.04>
- Schoevaerts, C., Goossens, D., D'Haemer, K., Van Dyck, H. and De Maeyer, L. (2011) 'The multitarget use of spirotetramat (Movento® 100 sc): simultaneous control of key pests in apples', *Acta Horticulturae*, (917), pp. 69–76. Available at:
<https://doi.org/10.17660/actahortic.2011.917.8>
- Schulte, P.M. (2015) 'The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment', *Journal of Experimental Biology*, 218(12), pp. 1856–1866. Available at:
<https://doi.org/10.1242/jeb.118851>
- Sharley, D.J., Hoffmann, A.A. and Thomson, L.J. (2008) 'The effects of soil tillage on beneficial invertebrates within the vineyard', *Agricultural and Forest Entomology*, 10(3), pp. 233–243. Available at: <https://doi.org/10.1111/j.1461-9563.2008.00376.x>
- Shaw, P. and Wallis, D. (2010) 'Susceptibility of the European earwig *Forficula auricularia* to insecticide residues on apple leaves', *New Zealand Plant Protection*, 63, pp. 55–59. Available at: <https://doi.org/10.30843/nzpp.2010.63.6568>
- Shaw, P.W. and Walker, J.T.S. (1996) 'Biological control of woolly apple aphid by *Aphelinus mali* in an integrated fruit production programme in Nelson', *Proceedings of the New Zealand Plant Protection Conference*, 49, pp. 59–63. Available at:
<https://doi.org/10.30843/nzpp.1996.49.11425>
- Simon, S., Riotord, D., Morel, K., Fleury, A. and Capowiez, Y. (2024) 'A shift towards softer pest management differently benefits earwig and spider communities in a multiyear experiment in apple orchards', *Pest Management Science*, 80(10), pp. 5088–5098. Available at:
<https://doi.org/10.1002/ps.8232>

- Solomon, M.G. (1992) 'Exploitation of predators in UK fruit and hop culture', *Phytoparasitica*, 20(S1), pp. S51–S56. Available at: <https://doi.org/10.1007/BF02980408>
- Stap, J.S., Mueller, T.F., Drukker, B., Blom, J., Mols, P.J.M. and Blommers, L. (1987) 'Field studies on the European earwig (*Forficula auricularia* L.) as predator of the woolly apple aphid (*Eriosoma lanigerum* Hausm.)', *Mededelingen - Universiteit Gent, Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen*, 52(2a), pp. 423–431. Available at: https://www.researchgate.net/publication/40174515_Field_studies_on_the_European_Earwig_Foricula_auricularia_L_as_predator_of_the_woolly_apple_aphid_Eriosoma_lanigerum_Hausm
- Switzer, C.M. and Combes, S.A. (2016) '*Bombus impatiens* (Hymenoptera: Apidae) display reduced pollen foraging behavior when marked with bee tags vs. paint', *Journal of Melittology*, 62, pp. 1–13. Available at: <https://doi.org/10.17161/jom.v0i62.5679>
- Tang, Y., Horikoshi, M. and Li, W. (2016) 'ggfortify: unified interface to visualize statistical results of popular R packages', *The R Journal*, 8(2), p. 474. Available at: <https://doi.org/10.32614/rj-2016-060>
- Thomson, L.J. and Hoffmann, A.A. (2006) 'Field validation of laboratory-derived IOBC toxicity ratings for natural enemies in commercial vineyards', *Biological Control*, 39(3), pp. 507–515. Available at: <https://doi.org/10.1016/j.biocontrol.2006.06.009>
- Toppa, R.H., Arena, M.V.N., da Silva, C.I., Marendy, P., de Souza, P. and da Silva-Zacarin, E.C.M. (2020) 'Impact of glues used for RFIDs on the longevity and flight muscles of the stingless bee *Melipona quadrifasciata* (Apidae: Meliponini)', *Apidologie*, 52(2), pp. 328–340. Available at: <https://doi.org/10.1007/s13592-020-00823-9>
- Tsiolis, K., Potts, S., Garratt, M., Tilston, E., Burman, J., Rintoul-Hynes, N. and Fountain, M. (2022) 'The importance of soil and vegetation characteristics for establishing ground-nesting bee aggregations' *Journal of Pollination Ecology*, 32, pp.186–200. Available at: [https://doi.org/10.26786/1920-7603\(2022\)682](https://doi.org/10.26786/1920-7603(2022)682)
- Van Meyel, S. and Meunier, J. (2020) 'Filial egg cannibalism in the European earwig: its determinants and implications in the evolution of maternal egg care', *Animal Behaviour*, 164, pp. 155–162. Available at: <https://doi.org/10.1016/j.anbehav.2020.04.001>
- Vasylyeva, N. and Harvey, J. (2021) 'Production and trade patterns in the world apple market', *Innovative Marketing*, 17(1), p. 16. Available at: [https://doi.org/10.21511/im.17\(1\).2021.02](https://doi.org/10.21511/im.17(1).2021.02)
- Venables, W.N. and Ripley, B.D. (2011) *Modern applied statistics with S*. New York; London: Springer.
- Vogt, H., Just, J. and Grutzmacher, A. (2010) 'Impact of four insecticides on the European earwig, *Forficula auricularia* L., in an apple orchard' *IOBC Working Groups "Integrated fruit protection in fruit crops": proceedings of the 7th International Conference on Integrated Fruit*

- Production*. Conference at Avignon (France), 27-30 October 2008. Available at: <https://iobc-wprs.org/product/impact-of-four-insecticides-on-the-european-earwig-forficula-auricularia-l-in-an-apple-orchard/>
- Wearing, C., Attfield, B. and Colhoun, K. (2010) 'Biological control of woolly apple aphid, *Eriosoma lanigerum* (Hausmann), during transition to integrated fruit production for pipfruit in Central Otago, New Zealand', *New Zealand Journal of Crop and Horticultural Science*, 38(4), pp. 255–273. Available at: <https://doi.org/10.1080/01140671.2010.524189>
- Weber, D.C. and Brown, M.W. (1988) 'Impact of woolly apple aphid (Homoptera: Aphididae) on the growth of potted apple trees', *Journal of Economic Entomology*, 81(4), pp. 1170–1177. Available at: <https://doi.org/10.1093/jee/81.4.1170>
- Wemmer, J.D. (2019) *Characterizing the dual transcriptomes of woolly apple aphid, Eriosoma lanigerum (hausmann), and its host, Malus domestica (borkh.), across a host resistance spectrum*. University of California, Riverside. Available at: <https://search.proquest.com/openview/943fd2a3bce52a11c12c6e5c49fc6371/1?pq-origsite=gscholar&cbl=18750&diss=y> (Accessed: 21 March 2025)
- Wickham, H. (2009) *ggplot2: elegant graphics for data analysis*. New York: Springer New York.
- Wickham, H., François, R., Henry, L., Müller, K. and Vaughan, D. (2023) 'dplyr: a grammar of data manipulation', R package version 1.1.4. Available at: <https://github.com/tidyverse/dplyr>
- Wirth, T., Le Guellec, R., Vancassel, M. and Veuille, M. (1998) 'Molecular and reproductive characterization of sibling species in the European earwig (*Forficula auricularia*)', *Evolution*, 52(1), pp. 260–265. Available at: <https://doi.org/10.1111/j.1558-5646.1998.tb05160.x>
- Wong, J.W.Y. and Kölliker, M. (2013) 'The more the merrier? Condition-dependent brood mixing in earwigs', *Animal Behaviour*, 86(4), pp. 845–850. Available at: <https://doi.org/10.1016/j.anbehav.2013.07.027>
- Wong, J.W.Y., Lucas, C. and Kölliker, M. (2014) 'Cues of maternal condition influence offspring selfishness', *PLOS ONE*, 9(1), p. e87214. Available at: <https://doi.org/10.1371/journal.pone.0087214>
- Wool, D. (2004) 'Galling aphids: specialization, biological complexity, and variation', *Annual Review of Entomology*, 49(1), pp. 175–192. Available at: <https://doi.org/10.1146/annurev.ento.49.061802.123236>
- Wool, D., Aloni, R., Ben-Zvi, O. and Wollberg, M. (1999) 'A galling aphid furnishes its home with a built-in pipeline to the host food supply', *Entomologia Experimentalis et Applicata*, 91(1), pp. 183–186. Available at: <https://doi.org/10.1046/j.1570-7458.1999.00482.x>
- Yu, L., Liu, Y., Bu, K., Wang, W.J. and Zhang, S. (2022) 'Soil temperature mitigation due to vegetation biophysical feedbacks', *Global and Planetary Change*, 218, p. 103971. Available at: <https://doi.org/10.1016/j.gloplacha.2022.103971>

Zeileis, A. and Hothorn, T. (2002) 'Diagnostic checking in regression relationships', *R News*, 2(3), pp. 7–10. <https://CRAN.R-project.org/doc/Rnews/>