HARPER ADAMS UNIVERSITY

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

A thesis submitted in partial fulfilment of the requirements of Harper Adams University for the degree of Doctor of Philosophy

By

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MSci

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Declaration

I, Hayden Tempest, hereby declare that this thesis is my own original work unless reported as such in the text. Information from other sources has been fully acknowledged and referenced in the text. None of this work has been submitted for publication or presented for the award of any other degree or diploma at any University.

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Abstract

Malus domestica (Bork; apple), is one of the most important fruit crops worldwide. The woolly apple aphid (*Eriosoma lanigerum*; Hausmann) has emerged as a serious pest of apple trees over the last 20 years thanks in part to the withdrawal of organophosphate insecticides. Information on the control of *E. lanigerum* by natural enemies is therefore valuable to apple growers. One important predator of *E. lanigerum* is *Forficula auricularia* (L.; common European earwig). This species has been shown to be an effective predator of *E. lanigerum* in apple orchards, but the control of *E. lanigerum* provided by *F. auricularia* appears to be inconsistent. This study aimed to investigate the distribution of *E. lanigerum* and *F. auricularia*, their interactions, and potential methods to discover more about the ecology of *F. auricularia*.

Commercial apple orchards in Kent (United Kingdom) were surveyed for the presence or absence of *F. auricularia* and *E. lanigerum* from individual trees. Generalised linear modelling was used to investigate which characteristics of trees and orchards were associated with the presence of each species. Molecular gut content analysis was also carried out to determine the frequency of *F. auricularia* predation of *E. lanigerum*. Evidence was found for a positive contribution by *F. auricularia* to *E. lanigerum* control, but only in conventionally managed orchards. Bare earth in the row bed of the orchards was associated with *F. auricularia* presence. Detectable DNA was only present in 5% of *F. auricularia* guts sampled. Unfortunately, the primers used for the molecular gut content analysis amplified *Ropalosiphum padi* DNA, so the precise frequency of predation of *E. lanigerum* could not be determined.

The impact of artificial *F. auricularia* shelters on the abundance of *F. auricularia* and *E. lanigerum* was investigated. The presence of artificial shelters led to an increase in the number of *F. auricularia* found during night-time searches, but did not lead to a measurable decrease in the number of *E. lanigerum* colonies.

Different glues were tested to determine their efficacy for attaching tags to *F. auricularia*, as well as their potential toxicity. Cyanoacrylate based glues are likely toxic to *F. auricularia*, but also the most effective for attaching tags. Thermoplastic glue was the most effective glue without an apparent toxic effect. Prototype mesocosms were designed and tested for their ability to collect data on *F. auricularia* behaviour using radio frequency identification (RFID). Minimal movement was detected in the prototype mesocosms, possibly as a result of flaws in the design, or due to the phenological stage of the individuals used for the study.

This study has shed light on the interactions of *F. auricularia* and *E. lanigerum* interactions within apple orchards. More research is required to understand the variable population dynamics of *F. auricularia*. Remote monitoring of *F. auricularia* in the field seems challenging using current technology but there are opportunities to study *F. auricularia* using mesocosm experiments.

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Glossary of Abbreviations

AIC	Akaike's Information Criterion
AMD	Azinphos-methyl and Codling Moth Mating Disruption
BBCH	Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie
bp	Base Pairs
BTP	Behaviour Transition Point
CO_2	Carbon Dioxide
cm	Centimetre
MD	Codling Moth Mating Disruption
Corp.	Corporation
°C	Degrees Celsius
DF	Degrees of Freedom
DNA	Deoxyribonucleic Acid
EAMU	Extension of Authorisation for Minor Use
EIR	Earwig Immobilisation Ring
et al.	*et alia*
Etc.	*Et cetera*
EPPO	European and Mediterranean Plant Protection Organisation
e.g.	*Exempli gratia*
FMD	Fenoxycarb and Codling Moth Mating Disruption
BRL	Freely draining slightly acid but base-rich loamy soils
FDAL	Freely draining slightly acid loamy soils
GHz	Gigahertz
g	Grams
GAA	Green Apple Aphid
i.e.	*Id est*
IPM	Integrated Pest Management
IOBC	International Organisation for Biological Control
kg	Kilogram
kg/cm^2	Kilogram per Square Centimetre
kHz	Kilohertz
LIDAR	Light Detection and Ranging
Ltd.	Limited
L	Litre
HGL	Loamy soils with naturally high groundwater
Max.	Maximum
MPa	Megapascal
m	Meter
µl	Microlitre
mg	Milligram
mL	Millilitre
mm	Millimetre
Min.	Minimum
Min/s	Minute/s
n.g.	Not given
NCBI BLAST®	National Center for Biotechnology Information: Basic Local Alignment Search Tool
pers. comm.	Personal Communications
PCR	Polymerase Chain Reaction
RFID	Radio Frequency Identification
RAA	Rosy Apple Aphid
RLCA	Rosy Leaf Curling Aphid

rpm	Rotations Per Minute
s	Seconds
IDLC	Slightly acid loamy and clayey soils with impeded drainage
SWLC	Slowly permeable seasonally wet and slightly acid but base-rich loamy and clayey soils
spp.	Species
m^2	Square metre
Std.	Standard
syn.	Synonym
UV	Ultraviolet
UK	United Kingdom
USA/US	United States of America
v.	Version
vs.	*Versus*
WAA	Woolly Apple Aphid

1. Literature review

1.1. General introduction

Malus domestica (Bork; apple) is, by tonnes produced, the second most abundant fruit crop in the world behind banana (O'Rourke, 2021; Vasylieva & Harvey, 2021). 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).

1.2. *Eriosoma lanigerum*

1.2.1. Distribution

The woolly apple aphid originated in North America (Theobald, 1920; Marcovitch, 1934; Barbagallo *et al.*, 1997; Beers, Cockfield & Gontijo, 2010). It is now found in every apple-growing region globally, including Europe, Australasia, and India (Jovičić, 2019). Woolly apple aphid is believed to have been spread primarily by infested rootstocks. It was introduced to the UK around 1796 (Theobald, 1920), with records of WAA in India as far back as 1889 (Gautam & Verma, 1983). When newly introduced to areas, there were often severe outbreaks. Theobald (1920) claimed "in 1810 no cider was made in Gloucestershire owing to this insect's ravages and it was feared the industry would die out all together", while Alspach and Bus (1999) said "the New Zealand apple industry was brought to the brink of ruin by this pest".

1.2.2. Lifecycle

In its native environment of North America, WAA is described as holocyclic on apple and American elm (*Ulmus americana*, L.). As with many aphid species, the primary host (American elm) is inhabited during the autumn and winter, and this is the only part of the lifecycle where WAA reproduces sexually. In the rest of the world, it is generally accepted that WAA exists year-round on apple, reproducing exclusively parthenogenically (anholocyclic; Blackman & Eastop, 1984). There have been reports of sexual morphs developing and laying eggs on apple in other parts of the world; however, these are currently believed to be incapable of reproduction and produce no viable eggs (Theobald, 1920; Asante, 1994; Sandanayaka & Bus, 2005; Dransfield & Brightwell, 2019). To further complicate matters, there is some debate over whether WAA is still holocyclic in North

America. Some researchers believe that *Eriosoma lanigerum* has lost host alternating behaviour in all environments, and reports of WAA on American elm should be attributed to closely related *Eriosoma* species rather than *E. lanigerum* (Blackman & Eastop, 1984; Dransfield & Brightwell, 2019).

The full lifecycle (which may have been completely lost) would be as follows (Sandanayaka & Bus, 2005): For much of the year, WAA exists as apterous (wingless) virginoparae (giving birth to live young) on apple. Both edaphic (root-dwelling) and aerial colonies of WAA occur during the warmer months, with new colonies being established by 1st instar apterous virginoparae nymphs (referred to as ‘crawlers’). These travel between the rootstock and scion of infested apple trees. The timing and direction of peaks in crawler migration appear to vary widely between orchards, and even more so between different regions of the world (Theobald, 1921; Heunis & Pringle, 2006; Beers, Cockfield & Gontijo, 2010). Some studies have reported spring migrations upwards and winter migrations downwards, while others have reported more-or-less continuous movement throughout the growing season, predominantly upwards. Once they have moulted into 2nd instars, the nymphs remain sessile and form into colonies. There are four nymphal instars alongside adulthood (Gautam & Verma, 1983). The apterous virginoparae will then go through multiple generations repeating this cycle during the summer (there may be as many as 20 generations in a year in the UK; Barbagallo *et al.*, 1997). Later in the growing season, alate (winged) morphs will start to be produced, in part because this is when colonies may start to become overcrowded. Some of these will still be virginoparae, dispersing and then producing apterous virginoparae, although these are reportedly less common (Asante, 1994; Sandanayaka & Bus, 2005; Beers, Cockfield & Gontijo, 2010). Other alate morphs will be sexuparae (aphids which parthenogenically give birth to sexual morphs), and travel to American elm. The alate sexuparae will then produce apterous sexuals on the American elm. The female sexual morphs are oviparae - the only egg-laying morph in the lifecycle. After sexual reproduction, the aphid will overwinter on American elm as eggs. In spring, fundatrices (females emerging from fertilised eggs) on American elm will produce alate virginoparae that will travel to apple and produce apterous virginoparae, restarting the cycle. For an overview of the lifecycle of *E. lanigerum*, refer to Figure 1.1.

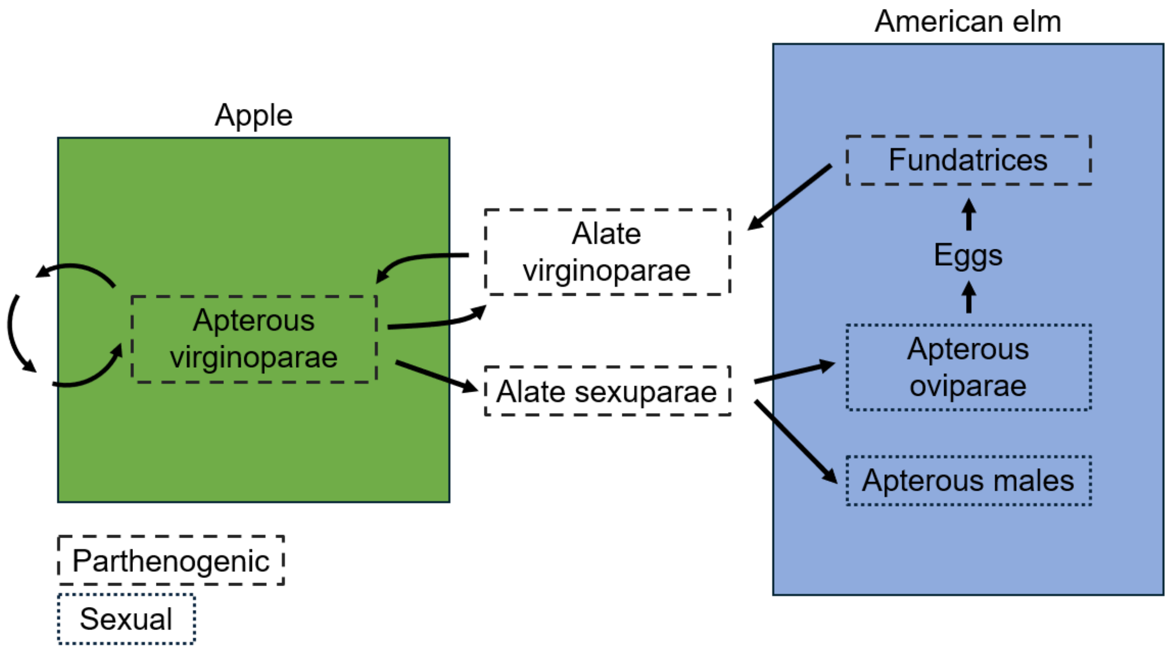

Figure 1.1. The full lifecycle of *Eriosoma lanigerum* on apple (*Malus domestica*; Bork and American elm (*Ulmus americana*, L.). Adapted from Godfrey (2024) and Sandanayaka and Bus (2005).

In practice, the vast majority of WAA (certainly outside of North America) exist as apterous virginoparae on apple. Alate virginoparae may help spread WAA between apple trees, although some researchers have argued that their contribution to dispersal is negligible due to low numbers (Asante, 1994; Beers, Cockfield & Gontijo, 2010). Rather than overwintering as eggs on American elm, WAA survives the winter as apterous virginoparae in sheltered positions on apple (Barbagallo *et al.*, 1997; Beers, Cockfield & Gontijo, 2010). Often, only edaphic colonies are thought to survive the winter, thus requiring crawler migration up the trunk in spring to re-establish aerial colonies each year (Theobald, 1920, 1921; Blackman Eastop, 1984; Heunis & Pringle, 2006; Hetherington, 2009; Beers, Cockfield & Gontijo, 2010; Stokwe & Malan, 2016). However, there is evidence to suggest that direct aerial-to-aerial recolonisation between years may be more significant than previously thought, with a greater proportion of the aerial WAA population surviving winter aboveground in cracks and crevices in the bark (Beers, Cockfield & Gontijo, 2010; Lordan *et al.*, 2015). The 1st and 2nd instar nymphs are noted as particularly cold-resistant, but all life stages of the apterous virginoparae have been reported year-round (Marcovitch, 1934; Asante, 1994; Barbagallo *et al.*, 1997; Damavandian & Pringle, 2007). Overwintering WAA, whether aerial or edaphic, do not appear to enter a dormant period, but reproductive activity does slow as temperatures decline (Theobald, 1920; Gautam & Verma, 1983; Damavandian & Pringle, 2007). The crawlers are the life-stage largely responsible for the dispersal of WAA, which may be the reason they show a relatively poor ability to spread between trees (Asante, Danthanarayana & Cairns, 1993; Brown & Schmitt, 1994). In temperate climates, crawlers take significantly longer to develop than the later nymphal stages, but this does not appear to be the case in warmer climates (Gautam & Verma, 1983; Asante, 1994). Woolly apple aphid aerial abundance peaks in spring and often shows a mid-season crash in the summer, which is usually attributed to high temperatures and the activity of *Aphelinus mali* (Haldeman; a parasitoid wasp discussed further below). There is then sometimes a resurgence of WAA in the autumn, as temperatures lower again (Brown & Schmitt, 1994; Heunis, 2001; Beers, Cockfield & Gontijo, 2010; Lordan *et al.*, 2015).

1.2.3. Basic biology

Apterous virginoparae WAA are 1.2 to 2.6 mm in length (Blackman & Eastop, 1984). Their bodies vary in colour from reds to browns to dark purples; however, these can be difficult to see as healthy aerial colonies are often completely obscured by a coating of thick white wax. As with all aphids, the stylet (mouthpart) of WAA pierces the tissue of the host plant and then navigates the interstitial spaces between cells (Tjallingii & Esch, 1993; Zhou *et al.*, 2021). Once it reaches sieve elements of the vascular tissue, the aphid repeatedly punctures cells as it tests them, before accepting a cell in the xylem or phloem and beginning to feed. During feeding, WAA saliva is released into the cells of the apple tree, which is believed to be responsible for the formation of galls. Galling is discussed further below; and may be necessary to allow WAA to feed at high densities without excessive competition (Wool *et al.*, 1999). Woolly apple aphid favours attacking the woody tissue of apple trees over the leaves or fruit, and has a preference for shoots and pruning wounds (Barbagallo *et al.*, 1997; Zhou *et al.*, 2021). The aerial colonies occur mainly on the trunk and lower canopy, and are almost always on the underside of branches rather than the top (Asante, Danthanarayana & Cairns, 1993). This shelters the aphid from rainfall, strong wind, and sunlight.

The eponymous ‘wool’ of WAA is a waxy substance excreted from the cuticle. The structure is quite complex, with filaments bundled into threads, then bundled into ‘skeins’, which themselves may be bundled into thicker strands (Smith, 1999). However, unlike some other wax-producing aphids, WAA skeins have a uniform and solid internal structure (as opposed to hollow or honeycombed tubes). These long skeins (or bundles of skeins) are the visible strands of wax which make WAA easy to identify in the field (Barbagallo *et al.*, 1997). They protrude from specialised collections of cells at the abdominal end of the aphid. Alongside these skeins, WAA are also coated all over in a thinner, powdery layer of wax. This layer of powdery wax is present in all life-stages of WAA, whereas the skeins are not produced by crawlers and are less pronounced in edaphic colonies (Theobald, 1920; Smith, 1999). The primary function of this wax is to act as an ultra-hydrophobic surface that prevents the honeydew excreted by WAA from coating them (Smith, 1999; Pike *et al.*, 2002). As orbs of honeydew are excreted, they are coated by the wax, forming droplets that can be strong enough for aphids to walk on without breaking (Pike *et al.*, 2002). This hydrophobicity is presumably beneficial for resisting rainfall as well as water-soluble insecticides. Other benefits of the wax have been speculated on, such as protection from natural enemies, or to provide a favourable microclimate, but more research is required to determine if these theories are true (Smith, 1999). It has been shown that *Marpissa marina* (Goyen; a species of jumping spider) struggles to visually identify wax-covered WAA compared to wax-less WAA; however, other predators such as *Forficula auricularia* (L.) appear to be undeterred by the presence of wax (Mueller, Blommers & Mols, 1988; Moss, Jackson & Pollard, 2006; Orpet, Crowder & Jones, 2019a).

1.2.4. Damage to apple

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). Galling 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 in close proximity to 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 galling 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*, Samuals 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).

1.2.5. Chemical control

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).

1.2.6. Natural enemies

There are a number of natural enemies of WAA which have been studied. One of the most important is *A. mali. Aphelinus mali* is a parasitoid wasp that reproduces exclusively on WAA (Peñalver-Cruz, Alvarez & Lavandero, 2020). Once WAA became a global pest of apple, *A. mali* was introduced almost everywhere that WAA occurs, in the first example of classical biocontrol used against an aphid (Dedryver, Le Ralec & Fabre, 2010). *Aphelinus mali* has a slightly higher optimum temperature than WAA, and so tends to appear later in the growing season than WAA. Once it does appear, *A. mali* numbers can rapidly increase within a season, which is believed to contribute to the frequently observed mid-season crash of WAA abundance. However, studies have suggested that on its own, *A. mali* can slow WAA population growth, but cannot induce a decline (Gontijo, Beers & Snyder, 2015; Quarrell, Corkrey & Allen, 2017). In order to get more complete control, *A. mali* must be present alongside generalist predators, which it synergises well with. When attacking WAA, *A. mali* is significantly more effective at parasitising smaller WAA colonies. Larger colonies may be protected by the density of aphids, and potentially the larger volume of obscuring wool (Mueller, Blommers & Mols, 1992; Shaw & Walker, 1996; Smith, 1999).

Generalist predators of WAA include coccinellid larvae, syriphid larvae, harvestmen, spiders, and *F. auricularia* (Gontijo, Beers & Snyder, 2013; Orpet, Crowder & Jones, 2019a). *Forficula auricularia* appears to be the most important of these and is discussed further below. Of the remainder, syriphid larvae are generally considered the most important (Gresham *et al.*, 2013; Bergh & Stallings, 2016; Panzeri *et al.*, 2024). There is evidence to suggest that despite not being tended by ants, *Formica* and *Myrmica* species may antagonise generalist predators of WAA and enhance their survival (Orpet, Crowder & Jones, 2019a). Stokwe & Malan (2016) provide a review of the use of entomopathogenic nematodes against WAA, which is an understudied area.

1.3. *Forficula auricularia*

1.3.1. Distribution

The common European earwig, *F. auricularia*, is the most widespread and abundant species in the order Dermaptera. Originally a native of Europe and parts of Asia, *F. auricularia* is now widespread due to human activity (Maczey, 2022). It is abundant in North America and Australasia, while its distribution in Africa is relatively unknown. In South America, the range of *F. auricularia* still appears to be expanding (Pavón-Gozalo *et al.*, 2011; Maczey, 2022). Within this global range, *F. auricularia* is found in a broad variety of environments, including agricultural crops. It is also a domestic pest and can frequently be found in the gardens of urban or sub-urban environments (Weems & Skelley, 1998). The distribution of *F. auricularia* within more natural environments is, by comparison, infrequently reported on. There is mixed information on the suitability of forests, while lower herbaceous and scrubby vegetation appears to be acceptable (Crumb, Bonn & Eide, 1941; Lamb, 1975; Lamb & Wellington, 1975; Happe *et al.*, 2018).

1.3.2. Lifecycle

The lifespan of *F. auricularia* is slightly longer than a year, leading to a few months of overlap between generations in spring. During their lifetime, *F. auricularia* undergoes five nymphal instars before adulthood; the first moult occurs before hatching and was thus only discovered recently (Tourneur, Cole & Meunier, 2020). Generally, *F. auricularia* hatch from clutches of approximately 50 eggs, remaining with their siblings and mother for a few weeks in a subterranean brood chamber (Kolliker, 2007; Van Meyel, Devers & Meunier, 2019; Tourneur & Meunier, 2020). There is variability in the exact timing and conditions that are associated with nymphs leaving the brood chamber, relating mainly to variations in the number of broods a female produces (discussed further below). Upon leaving the brood chamber, nymphs will be either 2nd or 3rd instars, and typically confine themselves to the ground while foraging and sheltering (Phillips, 1981). In apple orchards, *F. auricularia* will start to be found in trees when they begin moulting into 3rd and 4th instars, and reach peak arboreal abundance at 5th instar. There is a dramatic reduction in overall *F. auricularia* abundance accompanying the final moult into adulthood (Moerkens *et al.*, 2009). *Forficula auricularia* is thought to spend most of its time sheltering and foraging within trees for the rest of the growing season, with adults only beginning to leave in late-autumn and early winter (Phillips, 1981). At this time, they move back to the ground and form pairs to excavate brood chambers. Mating occurs before the excavation of brood chambers, and often with multiple conspecifics rather than solely the eventual nest-mate (Walker & Fell, 2001; Sandrin *et al.*, 2015). In late winter or early spring, the female oviposits and drives the male out of the chamber (Lamb, 1974; Lamb & Wellington, 1975). A brief overview of the *F. auricularia* lifecycle can be seen in Figure 1.2.

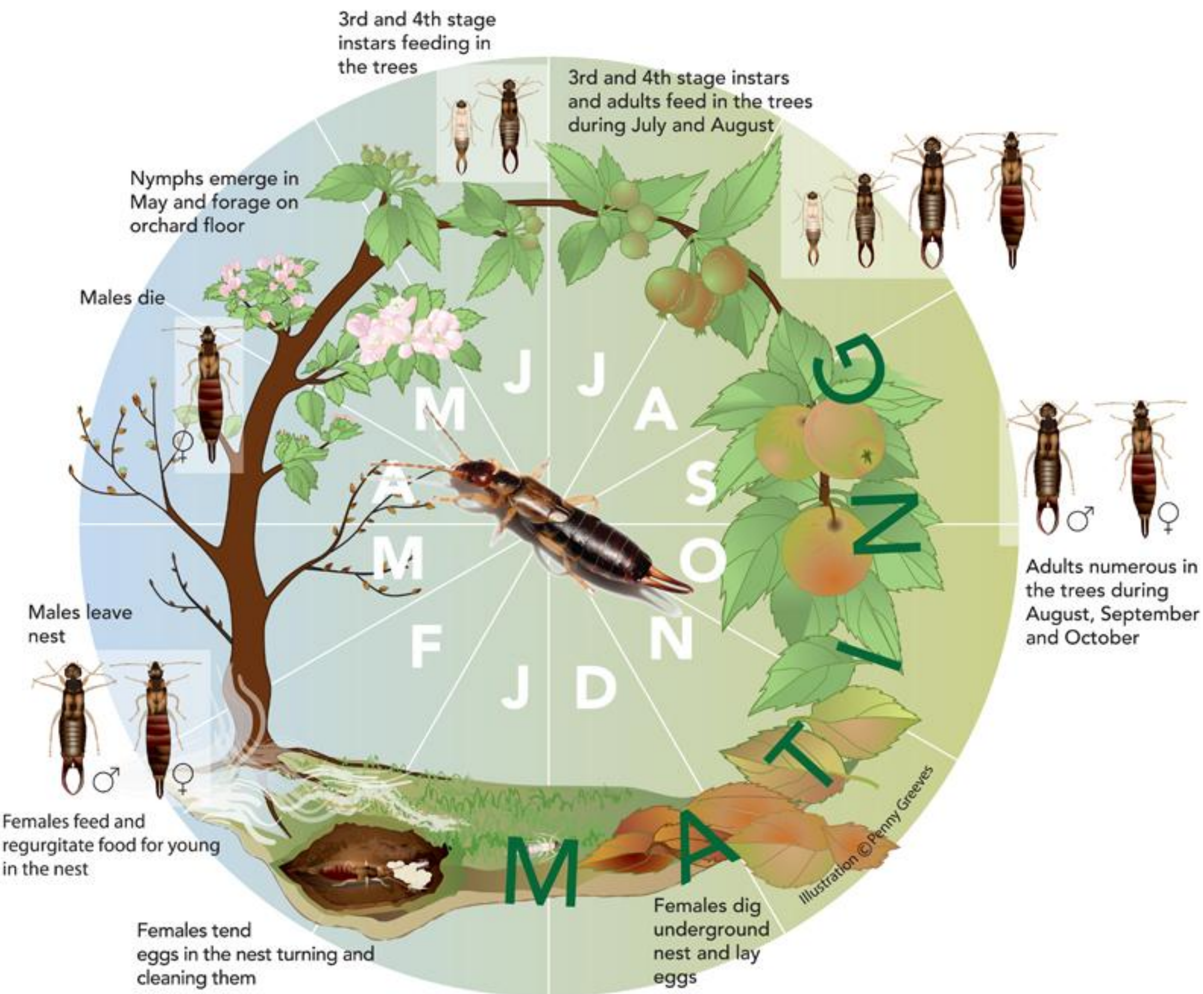

Figure 1.2. The annual lifecycle of *Forficula auricularia* in a UK apple orchard. Adapted from Greaves, P. (2018). Available at: https://archive.ahdb.org.uk/knowledge-library/earwig-friendly-spray-programmes-in-apple-and-pear-crops

Nest excavation and structure is quite varied between individuals. Typical depths are from 2 to 10 cm, and often the structure of the burrow is associated with a stone on the soil surface (Lamb, 1974). Between one and three chambers are excavated, and once the eggs are laid and the male driven off, the female will seal the nest while tending to her clutch. During this period, which takes place during winter, the mother does not feed. Mothers provide extensive care to their eggs, cleaning them to prevent fungal infections, relocating them frequently within the nest (which is believed to regulate their temperature), defending them from attack, and re-collecting them into a single mound if scattered (Lamb, 1974; Kolliker, 2007; Kölliker & Vancassel, 2007; Mas, Haynes & Kölliker, 2009; Meunier *et al.*, 2012; Boos *et al.*, 2014; Koch & Meunier, 2014; Wong, Lucas & Kölliker, 2014; Kramer, Thesing & Meunier, 2015; Tourneur *et al.*, 2022; Van Meyel & Meunier, 2022). Studies have shown that females will care for other *F. auricularia* eggs if presented with them (Van Meyel, Devers & Meunier, 2019). While not always the case, *F. auricularia* mothers will sometimes forage and return to their hatched young and provision them with food (Kolliker, 2007; Kölliker & Vancassel, 2007; Staerkle & Kölliker, 2008; Van Meyel, Devers & Meunier, 2019; Tourneur & Meunier, 2020).

The degree and duration of maternal care depends on the number of broods a mother has (Meunier *et al.*, 2012). When originally described, *F. auricularia* was thought to produce only a single brood each year. However, it was discovered that in many populations, at least a portion of *F. auricularia* lay two broods of eggs (Beall, 1932; Wirth *et al.*, 1998). In rare cases, even three broods have been reported, although this is usually only seen in populations reared in the laboratory. Double-brood mothers will abandon their initial clutch immediately after hatching, disperse, and then excavate a new chamber to lay their second clutch (Moerkens *et al.*, 2009). It has been demonstrated that in some cases, double-brood and single-brood populations of *F. auricularia* are different subspecies which cannot interbreed (Wirth *et al.*, 1998). Double brood populations were dubbed species B, while the original univoltine species is referred to as species A. Recent taxonomic study has suggested that there may be as many as four subspecies in the *F. auricularia* complex, with three of these being morphologically indistinguishable (González Miguéns *et al.*, 2020). The question of which subspecies is present is often ignored during research, with the originally identified species A and B typically only being distinguished by the number of broods. This is despite the fact that species A can produce either one or two broods (species B always produces at least two), and there appear to be significant differences in other aspects of their life history such as dispersal and cold hardiness (Moerkens *et al.*, 2010, 2012).

1.3.3. Basic biology

Forficula auricularia have a typical adult body length of 12 to 15 mm (Weems & Skelley, 1998). The abdomen ends in a distinctive pair of cerci/forceps for both males and females, although the shape of the cerci differs between the sexes in adulthood. In males, the cerci are strongly curved, and have crenulated teeth basally, with two morphs that vary dramatically in cerci length (Tomkins, 1999; Walker & Fell, 2001; Rantala, Roff & Rantala, 2007). The cerci of females are thinner, straighter, and more consistent in shape and length. The cerci of nymphal instars resemble those of adult females, although they are thinner and weaker. The abdomen of adult males tends to be more dorsoventrally flattened in comparison with females, particularly when females are gravid. Females also tend to be heavier, although this is more pronounced later in the season (Walker & Fell, 2001; Le Navenant *et al.*, 2021). The adults are a dark brown colour, and notably shiny, with yellowy-orange legs and elytra. Nymphs are initially pale, almost transparent, and develop colour slowly as they moult (Figure 1.3). *Forficula auricularia* are notably oily, and when handled with bare skin they leave a brown stain which has a distinctive smell, and which does not immediately wash off. This may be due to the defensive quinone spray *F. auricularia* possesses (Eisner, 1960). Perhaps because of this, they are particularly difficult to mark with fluorescent powders or paints, though not impossible (Lamb, 1974, 1975; Phillips, 1981; Moerkens *et al.*, 2010).

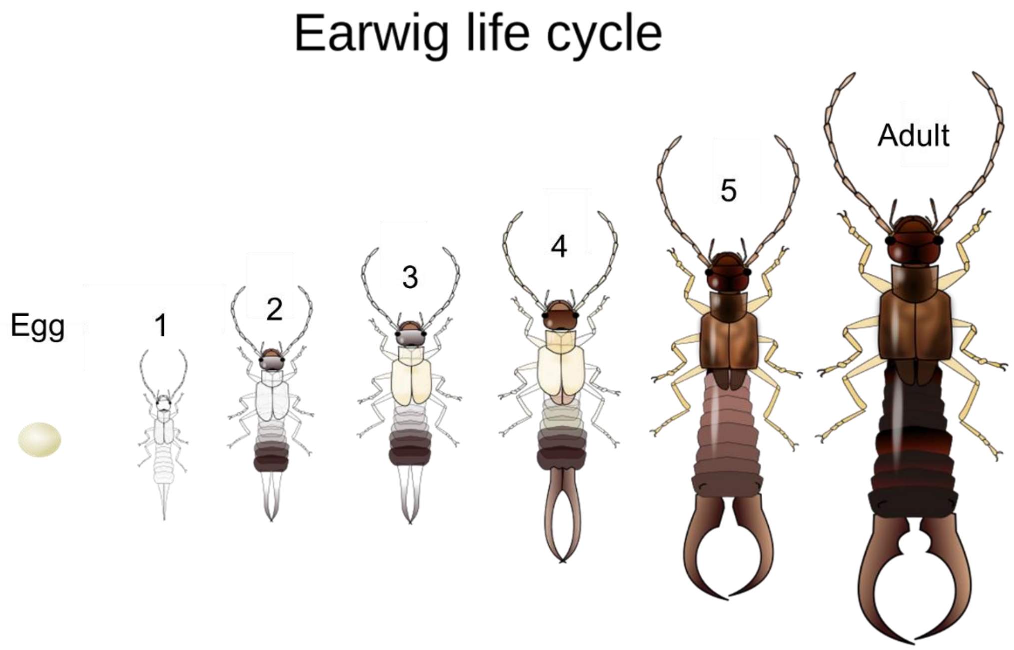

Figure 1.3. The appearance of the life stages of *Forficula auricularia,* going from left to right. The five instars are shown, with the final adult form on the right. Note that the cerci here are characteristic of males. Adapted from BugBoy (2009). Available at: https://commons.wikimedia.org/wiki/File:Earwig_life_cycle_2.svg

As a member of the order Dermaptera, *F. auricularia*'s forewings are not functional in flight, rather forming a pair of protective elytra. Unlike the hardened elytra of Coleoptera, these are leathery and still maintain some flexibility. The hindwings are folded beneath the forewings, with the posterior tips protruding from underneath the forewings. The folding of Dermapteran flight wings is unique and extremely efficient, with the highest folding ratios reported for any insect (Deiters, Kowalczyk & Seidl, 2016; Faber, Arrieta & Studart, 2018; Saito *et al.*, 2020). In *F. auricularia* these wings are functional. Nevertheless, it is rare to observe *F. auricularia* in flight, so much so that they can be effectively excluded from tree canopies with 'tanglefoot' sticky bands on the trunk. The importance of flight to *F. auricularia* biology is therefore something of a mystery. There are academic records of mass flights of *F. auricularia* (Buzzetti *et al.*, 2003; Pavón-Gozalo *et al.*, 2011), but the significance of these to *F. auricularia* distribution is unknown. It is possible that higher temperatures are more conducive to *F. auricularia* flight (Crumb, Bonn & Eide, 1941; Buzzetti *et al.*, 2003).

Forficula auricularia are nocturnal, and as a result, field observations of their behaviour are challenging to collect. During the day they exhibit strong positive thigmotaxis, selecting tight, dark spaces to shelter. While sheltering, *F. auricularia* shows aggregation behaviour, with numerous conspecifics taking refuge together if possible. This is generally believed to be mediated by an aggregation pheromone, in the form of a cuticular hydrocarbon which both coats *F. auricularia* and is deposited on surfaces they contact, although studies investigating this have had contradictory results (Walker, Jones & Fell, 1993; Hehar, 2007; Hehar, Gries &

Gries, 2008; Quarrell *et al.*, 2016). It has been suggested that the response of *F. auricularia* to the pheromones of conspecifics depends on the sex of both individuals as well as their life stages (Quarrell *et al.,* 2016). Regardless, *F. auricularia* shows a clear preference for previously used or currently occupied shelters (Lamb, 1975; Phillips, 1981; Sauphanor & Sureau, 1993; Walker, Jones & Fell, 1993; Evans & Longépé, 1996; Lordan *et al.*, 2014; Hanel *et al.*, 2023). Currently, it is believed that these aggregations are transient, with no lasting bonds between the members of an aggregation, and no fidelity for a particular refuge shown by individuals (Lamb, 1975). *Forficula auricularia* is also reported to perform social grooming while in aggregations (Lamb, 1975).

Due to the difficulty in studying *F. auricularia* foraging in situ, much of the information on their diet comes from laboratory-based feeding experiments or gut content analysis. *Forficula auricularia* is 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), *F. auricularia* 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*, Degreer; 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 *F. auricularia* feeds 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 *F. auricularia* 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 *F. auricularia*, 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 *F. auricularia* 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 *F. auricularia* (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 *F. auricularia* (Lamb, 1975; Gobin *et al.*, 2006). Currently, the navigational ability of *F. auricularia* 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 *F. auricularia* mothers to forage and return to their brood chamber to provision for their offspring suggests that it is possible for *F. auricularia* to relocate sites. Also, when released into apple and pear orchards, *F. auricularia* showed very low levels of dispersal (Moerkens *et al.*, 2010). Ninety five percent of *F. auricularia* 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 *F. auricularia* frequently return to the same shelter simply because they never move far from it (Phillips, 1981; Moerkens *et al.*, 2009).

1.3.4. Role in orchards

Due to their omnivorous diet, *F. auricularia* 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 *F. auricularia* have been researched (Crumb, Bonn & Eide, 1941; Maczey *et al.*, 2016). In other crops, namely apples, pears, citrus fruit, and kiwifruit, *F. auricularia* is 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 *F. auricularia*, and while some secondary damage to fruit or to the trees may occur, this is outweighed by their consumption of more serious pests. As *F. auricularia* is considered as both a predator and a pest, multiple researchers have investigated the possibility of removing *F. auricularia* from crops where it causes damage and releasing it into pome fruit orchards where it may control pest species (Evans & Longépé, 1996; Hanel *et al.*, 2023).

1.3.5. Response to orchard management

Spinosad, indoxacarb, chlorpyrifos, deltamethrin, azinphos-methyl, cypermethrin, diazinon, kaolin particles, thiacloprid, carbaryl, and flonicamid have all been shown to induce significant mortality in adult *F. auricularia*, 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, emamectin benzoate are less harmful to adult *F. auricularia* (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, 2008; 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 *F. auricularia* may significantly slow the growth of immature *F. auricularia*. 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 *F. auricularia* 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 *F. auricularia* tends 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 *F. auricularia* in organic and IPM orchards. Transgenerational studies on unexposed offspring with parents from different management types show that *F. auricularia* experience some intergenerational effects from insecticide use, but in general *F. auricularia* generations seem to recover well if insecticide sprays are stopped (Le Navenant *et al.*, 2021). There is evidence that *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* appear to overwinter outside of orchards altogether (Romeu-Dalmau, Espadaler & Piñol, 2016).

1.3.6. Natural enemies

The natural enemies of *F. auricularia* have received comparatively little attention, especially in recent years. Two tachinid flies parasitise *F. auricularia*, *Triarthria setipennis* (Fallén) and *Ocytata pallipes* (Fallén; Crumb, Bonn & Eide, 1941; Phillips, 1981; Moerkens *et al.*, 2012; Maczey *et al.*, 2016). A third has been reported, *Zenilla nemea* (Meigen), but the author has been unable to find a modern synonym for this species (Phillips, 1981). Additionally, Moerkens *et al.* (2012) report *Triarthria setipennis* and *Triarthria spinnipennis* as separate species, but these have been treated elsewhere as synonymous (Smith, 1989; Herting, 2017). *Ocytata pallipes* lays eggs on plants which show signs of *F. auricularia* feeding, with ingestion of the eggs leading to *F. auricularia* parasitisation (Kuhlmann, 1994). *Triarthria setipennis* lays eggs close to *F. auricularia*, which immediately hatch, and the young burrow into the nearby *F. auricularia* through the intersegmental skin (Kuhlmann, 1995). The rate of parasitisation by these two species varies between 0 and 20%, but is often less than 10% (Phillips, 1981; Moerkens *et al.*, 2012). Both tachinids have a high rate of hyperparasitisation by *Dibrachys cavus* (Walker) and *Phygadeuon vexator* (Thunberg), two species of wasp (Phillips, 1981). Moerkens *et al.* (2012) remark that attempts to control *F. auricularia* using releases of *T. setipennis* and *O. pallipes* have not been successful.

Although other fungal pathogens have been reported to be associated with *F. auricularia* (*e.g.* Coulm & Meunier, 2021), the most important fungal disease affecting *F. auricularia* is *Zoophthora forficulae* (Giard; syn. *Entomophthora forficulae;* Crumb, Bonn & Eide, 1941; Phillips, 1981; Goettel, Eilenberg & Glare, 2010). Crumb, Bonn & Eide (1941) state that nymphs are more susceptible to *Z. forficulae* than adults, and that in “wet, chilly weather” mortality from this fungus can be high. In contrast, Phillips (1981) found no clear pattern of incidence with temperature and rainfall, and only a single plot where the incidence of *Z. forficulae* was higher than 3%, although they note that fungicides were applied to all studied plots during the year of their study.

Forficula auricularia is also parasitised by nematodes (Crumb, Bonn & Eide, 1941; Phillips, 1981). Herbison *et al.* (2019) demonstrated the ability of adult *Mermis nigrescens* to manipulate host *F. auricularia* to enter water in order to complete the parasite’s life cycle. The author has observed 2 of 870 dissected *F. auricularia* to contain lengthy nematode worms, although their appearance did not closely match *M. nigrescens*. The guts of *F. auricularia* are reported to frequently contain gregarines, eukaryotes from the phylum Apicomplexa (Crumb, Bonn & Eide, 1941; Phillips, 1981). *Forficula auricularia* appears to be capable of surviving with high numbers of gregarines inside their gut, suggesting they may not be a particularly harmful parasite.

Birds appear to be the most common vertebrate predators of *F. auricularia*, in particular starlings (*Sturnus vulgaris*, L.) and little owls (*Athene noctua,* Scopoli; Crumb, Bonn & Eide, 1941; Lamb, 1975; Phillips, 1981; Gobin *et al.*, 2006). Crumb, Bonn and Eide (1941) also mention toads and snakes as predators, and note that leaving poison bait for *F. auricularia* can lead to numerous dead snakes through the ingestion of poisoned *F. auricularia*. Ground beetles and ants can also attack *F. auricularia*, although the forceps of *F. auricularia* are an effective defence against other insects (Crumb, Bonn & Eide, 1941; Eisner, 1960). Peusens *et al.* (2009) found no clear effect of bird exclusion on *F. auricularia* abundance, in contrast with Lamb (1975), who suggested protection from birds was the key benefit of increased shelter for *F. auricularia*. They also found no effect on mortality from the exclusion of small mammals over winter. The author has observed *F. auricularia* caught in spiderwebs, although spiders would sometimes occupy refuge traps (particularly the design used in 2022; Chapter 2) alongside *F. auricularia*.

Cannibalism has been put forward as an important factor in *F. auricularia* population ecology, as an explanation for the poor survival from 5th instar to adulthood, but there is a lack of direct observation to support this (Moerkens *et al.*, 2009, 2012). Intraspecific aggression in *F. auricularia* during the phase where nymphs have hatched and mothers provide care is a complicated topic. Mothers show the same level of maternal care to adopted eggs and offspring as they do for their own young (Van Meyel, Devers & Meunier, 2019). However, when starving, *F. auricularia* nymphs will cannibalise each other, and are more likely to cannibalise unrelated nymphs (Dobler & Kölliker, 2010). The rate of cannibalism is further influenced by size, with larger, heavier, nymphs tending to win antagonistic interactions (Dobler & Kölliker, 2011). Brood mixing appears to be driven by the 'invading' nymphs, with the maternal female showing no ability/proclivity to prevent new individuals joining her brood. Nymphs in good condition which have had their mother experimentally removed tended to join broods with an attending female, thus benefitting from maternal care and with a minimal risk from cannibalism (Kölliker & Vancassel, 2007; Wong & Kölliker, 2013). Nymphs in poor condition were more at risk of being cannibalised if they joined a brood, and so mixed less frequently. However, the majority of studies on cannibalism discussed above occurred in unnatural conditions, and involved the early instars of *F. auricularia*. High rates of cannibalism between adults and 5th instars therefore remains speculative.

1.4. *Forficula auricularia* predation of *Eriosoma lanigerum*

1.4.1. Containment studies

Studies investigating interactions between *F. auricularia* and WAA have involved placing both species into confined arenas. For example: Asante (1995) investigated the functional response of *F. auricularia* to WAA in Petri dishes in the laboratory. They found a type 2 functional response for *F. auricularia*, meaning the rate of consumption plateaus with increasing prey density. *Forficula auricularia* ingested more younger instar WAA than older WAA.

Bischoff *et al.* (2024) investigated the interactions between *F. auricularia* population density, environmental complexity, and *F. auricularia* predation of WAA. They confined populations of WAA and *F. auricularia* to individual branches of varying structural complexity. They showed more structurally complex branches were harder for *F. auricularia* to search, and so WAA was more likely to survive in these complex environments. However, this effect could be overcome by increasing the *F. auricularia* population density.

Carroll, Walker and Hoyt (1985) primarily looked at earwigs as a control method for *A. pomi*, but part of their study involved caging aphids on apple rootstock stool beds, after the application of insecticides. They found that the earwigs prevented the resurgence of *A. pomi,* but had no significant effect on the WAA colonies already established there.

The containment studies described in this section provide some of the most straightforward and unambiguous evidence for *F. auricularia* consumption and control of WAA. Carroll, Walker and Hoyt (1985) are notable for finding a lack of WAA control when *F. auricularia* were confined to rootstocks with them. This may have been due to testing the effect of *F. auricularia* 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 *F. auricularia* was 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), *F. auricularia* 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 *F. auricularia* when it comes to biocontrol. While methods can be imagined for enhancing the efficiency of a given number of *F. auricularia*, such as providing shelter close to WAA colonies, or removing alternative sources of food, simply increasing the number of *F. auricularia* seems more practical.

1.4.2. Exclusion studies

Studies investigating the impact of excluding *F. auricularia* from some portion of the apple tree canopy on damage caused by WAA have been completed. For example: Stap *et al.* (1987) completed several field experiments to assess *F. auricularia* feeding on WAA. In two similar experiments, they excluded *F. auricularia* from tree canopies using sticky bands, and then experimentally manipulated the number of *F. auricularia* in the canopies. In two further experiments, they introduced WAA colonies to orchards and again manipulated *F. auricularia* numbers. In all cases, they showed that in trees where *F. auricularia* numbers were reduced through exclusion and removal, WAA infestations were more severe. In addition, the artificially introduced WAA colonies were located and destroyed more rapidly when *F. auricularia* were present at high densities (approximately > 3 *F. auricularia* per tree, although this varied over time).

Nicholas, Spooner-Hart and Vickers (2005) compared orchards under an IPM spraying regime which used codling moth mating disruption (MD; using sex pheromone dispensers), with orchards that used fenoxycarb (an insect growth regulator) and codling moth mating disruption (FMD), and orchards that used the broad-spectrum insecticide azinphos-methyl (an organophosphate) and the mating disruption (AMD). They also used sticky bands to stop crawling predators from entering some of the trees in the MD and FMD treatments (they ensured these were infested with WAA) and then compared the extent of WAA on these trees to the unbanded ones. They found that while WAA numbers started out similar in all three treatments, they increased later in the season and stayed significantly higher in the AMD orchards. They found a strong negative correlation between the number of earwigs taking refuge in a tree and the level of WAA infestation. Also, when earwigs were excluded using the sticky bands, WAA infestation levels were significantly higher. As well as earwigs, *A. mali* was found to benefit from the lack of broad-spectrum insecticides. *Aphelinus mali* probably played an important role in controlling WAA in the MD and FMD orchards. However, it would not have been excluded by the sticky bands, so earwigs were considered the key species responsible for WAA control in the two IPM strategies. The authors found a significant interaction between apple cultivar and the ability of earwigs to effectively control WAA, as Red Delicious, a more susceptible variety, was not effectively cleared of WAA in all seasons. The authors suggested a minimum of five *F. auricularia* per tree was required for WAA control.

Orpet, *et al.* (2019b) applied sticky bands to apple trees to prevent WAA in the rootstock from migrating into the canopies, in order to reduce WAA infestation levels. Instead, trees with sticky bands tended to have more WAA colonies later in the season (sticky bands alone did not have a significant effect but showed a significant interaction with time). The authors identified earwigs as the likely cause of this trend, as sticky bands prevented earwigs from foraging in the canopies, and significantly fewer earwigs were found in shelters attached to banded trees than control trees.

Lordan *et al.* (2015) applied three treatments to branches of trees which had been infested with WAA the previous year. One third were covered in cloth bags to isolate them from recolonisation by edaphic WAA crawlers and predators, one third were isolated using sticky bands, and one third were left as controls. However, in 16 of 25 branches which were covered in a bag, *F. auricularia* were recorded to have gained entry. These 16 branches had significantly lower levels of WAA infestation than the bags that did not contain *F. auricularia*. The sticky banded and control branches also had significantly lower levels of WAA than the unbroken bagged treatments, with the authors noting the sticky bands used did not exclude *F. auricularia*. This study provided evidence for direct aerial-to-aerial WAA recolonisation across years in the Mediterranean environment.

Gontijo, Beers and Snyder (2015) looked at the suppression of WAA in a series of exclusion-cage experiments. While earwigs were not explicitly studied, they were included in the 'generalist predators' guild in the study. The authors found evidence for a low level of antagonism between predators and the parasitoid *A. mali*, which proved insignificant for the control of WAA. Instead, there appeared to be a great deal of complementarity between the predators and *A. mali*, with the effective control of WAA colonies only being found in plots where neither guild was excluded. *Aphelinus mali* alone was capable of significantly slowing WAA population growth but not actually reducing their number.

Mueller, Blommers and Mols (1988) examined three plots of apple trees with different densities of earwig (monitored and released using refuge trapping). They found that in the high and intermediate earwig density plots there were significantly fewer WAA colonies than in the third plot, where earwigs were excluded. They also showed that artificially introduced test colonies of WAA were located and destroyed in significantly less time when earwigs were not excluded. It is worth noting that *A. mali* was present in the orchards used for this experiment.

Unlike some of the other study designs discussed, all exclusion experiments studying *F. auricularia* 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 *F. auricularia*. This is highlighted by the fact that Orpet, *et al.* (2019b) unintentionally excluded *F. auricularia* 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 *F. auricularia* predation and that of other species, and are thus confident that *F. auricularia* was 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 *F. auricularia* into some of the banded canopies, thus demonstrating unambiguously that *F. auricularia* was 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 *F. auricularia* in controlling WAA, and are therefore relevant to the section below (Stap *et al.*, 1987; Mueller, Blommers & Mols, 1988; Nicholas, Spooner-Hart & Vickers, 2005).

1.4.3. Correlation studies

Several studies have utilised refuge trapping to monitor *F. auricularia* abundance and then tested if this was correlated with WAA abundance. For example: Quarrell, Corkrey and Allen (2017) looked at a variety of organic, IPM, and conventional orchards, and monitored various ecological groups within the insect community, as well as WAA numbers. They found that, after management type, earwig numbers early in the season were the best predictor of WAA infestation scores. If 15 or more earwigs were trapped per tree in the first seven weeks, then WAA scores remained below the economic threshold. If earwig numbers dropped below this, then *A. mali* numbers became important, but on its own *A. mali* was not sufficient to control WAA.

Hanel *et al.* (2023) used refuge traps to remove *F. auricularia* from cherry and apricot orchards, and released them into pear and apple orchards. This failed to significantly reduce the number of *F. auricularia* in the cherry and apricot orchards, where they are a pest, but did increase *F. auricularia* numbers in one orchard where they had previously been close to absent. When releasing the captured *F. auricularia*, besides the control treatment, they also tested two release strategies. One was a mass release early in the season, while the other was a more gradual and continuous release. In the first year of the study there were no significant differences between any of the treatments. In the second year, the mass release led to significantly fewer WAA than the continuous release, with the control plot being intermediate.

Helsen *et al.* (2007) studied *F. auricularia* and WAA populations in IPM and organic orchards. They found a negative correlation between *F. auricularia* abundance and WAA infestation in both management types. They also captured more *F. auricularia* in organic orchards. It is worth noting that Helsen *et al.* (2007) do not present any statistical analysis of their data, instead relying on summary statistics.

Alins *et al.* (2023) used artificial shelters and augmentative releases to increase the abundance of *F. auricularia* in orchard plots, and compared these to plots with no shelters or release. The *F. auricularia* were introduced inside of the shelters, which were placed immediately next to a WAA colony. They showed that in the second and third years of these treatments, the length of the colony directly next to the shelter was significantly reduced. However, there was no significant difference in the first year of release, and there was no significant difference in the number of WAA colonies in the trees as a whole. Predation by *F. auricularia* did not lead to a reduction in parasitisation by *A. mali*.

Marshall and Beers (2021, 2022) tested the effects of full-block net enclosures designed to stop codling moth. They found that enclosed apple trees had higher WAA levels than control trees, despite earwigs being unaffected by the nets, and *A. mali* abundance was higher inside the netted orchard blocks. The authors noted that this result was unexpected, but stated that the exclusion of lacewings and syrphids may have been responsible for this finding. As the data is presented in cumulative insect-days, it is slightly unclear exactly how abundant *F. auricularia* was in the experiment; however, the results seem to indicate large numbers of *F. auricularia* were present.

Happe *et al.* (2018) studied the impacts of orchard management and landscape factors on both earwig and WAA abundance in Spanish and German apple orchards. They found in both countries *F. auricularia* abundance was similar in IPM and organic orchards (in Spain the earwig *F. pubescens*, Gené, was significantly more abundant in organic orchards). In one German orchard, for one month, there was a significant negative correlation between earwig abundance and WAA infestation, but in all other months there was no significant correlation. Interestingly, this study also found a negative effect of woodland habitats on *F. auricularia* abundance in German IPM orchards specifically, which the authors noted runs counter to some previous studies. Happe *et al.* (2018) suggested the older orchards used in their study already had established earwig populations and so did not require woody habitats to act as migration corridors; instead, these habitats may have acted as more attractive areas that earwigs migrated to. No other landscape factor influenced *F. auricularia*'s abundance in either country. For WAA, organic orchards had higher levels of infestation in Spain, while in Germany having larger proportions of apple orchard in the surrounding 1 km was the only significant factor for WAA abundance.

Orpet *et al.* (2019a) manipulated *F. auricularia* numbers in three types of orchard plot: control plots, *F. auricularia* removal plots, and *F. auricularia* inundation plots. Across all the orchards used in the experiment, the inundation plots contained fewer WAA colonies, with lower peaks in abundance. They also conducted molecular gut content analysis on *F. auricularia* taken from the inundation plots, testing for WAA DNA specifically and sequencing any available DNA to match to species. The frequency of predation (as detected by WAA DNA) differed between the different orchards but did not correlate with WAA abundance. The percentage of *F. auricularia* testing positive for WAA DNA ranged from 0% to peaks of approximately 90%. Use of next generation sequencing showed a wide variety of species were consumed by *F. auricularia*, with the highest diversity in fungal taxa. There was evidence that all *F. auricularia* consumed at least some of the apple tree (either fruit or foliage).

Overall, the majority of these studies show that *F. auricularia* abundance is negatively correlated with WAA abundance, with threshold values of *F. auricularia* 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 *F. auricularia* (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 *F. auricularia* (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 *F. auricularia* 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 *F. auricularia*, the use of refuge trapping to monitor these populations may have altered the population dynamics of *F. auricularia*, rather, 'experimentally unaltered' means there was no attempt to deliberately change the number of *F. auricularia* between different treatments). Studies which used augmentative releases of *F. auricularia* may be less applicable to the conditions in a standard commercially managed orchard. Of the studies which did not find significant negative correlations between *F. auricularia* and WAA abundance, Happe *et al.* (2018) provided no discussion of this result. The mean number of *F. auricularia* per tree varied from 3 to 27.1, so there were occasions where *F. auricularia* 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 *F. auricularia* and *A. mali* were present. As mentioned above, they attribute this to the exclusion of other aphid predators, particularly *Heringia* spp. of syraphid flies. *Heringia* spp. would not have been excluded in sticky band experiments, so this does not discount the effectiveness of *F. auricularia*, 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 *F. auricularia* take effect over multiple years. This is important, as it suggests early season abundance of *F. auricularia* is important, simply increasing *F. auricularia* 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 *F. auricularia* predation of WAA, and is therefore relevant to section below.

1.4.4. Other studies

Several studies have used methods not covered by the previous sections. For example: Orpet, Crowder and Jones (2019b) used video recordings of WAA colonies to assess the levels of predation by different species. They found that earwigs made the highest number of attacks and were present in orchards to attack WAA early in the growing season before other predator species arrived. Coccinellid larvae (unidentified species) spent the longest cumulative time attacking WAA colonies, due to their longer attack duration when compared with earwigs. There was no assessment in this study of the impact of each species on WAA, so the number of attacks and time spent attacking are the only indication of which species might be most important for WAA control. Earwigs were never observed antagonising other predators; however, they themselves were often antagonised by ants (*Formica* and *Myrmica* species). When this occurred, the earwigs would move away, and the number of these ant-earwig interactions was negatively correlated with the number of earwig attacks on WAA colonies.

Gobin *et al.* (2008a) investigated the phenology of *F. auricularia* in apple orchards. They used this data to make predictions about their potential impact on various pests of apple based on the timing of emergence and population peaks. They suggested that the phenology of *F. auricularia* was “ideal” to help control WAA.

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 *F. auricularia* predation and efficacy in the field. In particular, the presence of WAA DNA in *F. auricularia* guts at low WAA abundances highlights the strength of *F. auricularia* 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.

1.5. Radio frequency identification

1.5.1. General introduction to radio frequency identification

Given the difficulty in observing *F. auricularia* during its 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.

Tags are attached or implanted into study animals. When detected/read by the antenna, the system records the unique identity of the tag/animal, as well as the time at which it was detected (Reynolds & Riley, 2002). Two antennas can be combined in sequence to create a ‘directional reader’. The order in which the two antennas detect the tag gives the direction an organism is travelling in a single plane (Ai & Takahashi, 2021). The ‘read range’ or ‘detection range’ are interchangeable terms describing the maximum distance a tag can be from an antenna and still be detected. Radio Frequency Identification systems used in ecology range from 30 kHz all the way to 2.5 GHz for high performance systems (Reynolds & Riley, 2002).

There are two main types of RFID tags, passive and active (Senadeera *et al.*, 2013). Active tags contain an internal battery and periodically transmit a signal to be detected by the antenna. Passive tags, by contrast, contain no internal power source, instead relying on the magnetic field of the antenna to power them. This leads to several trade-offs between these types of tags. Active tags will have dramatically longer read ranges than passive tags; however, the need for a battery means they are bulkier and heavier, and they also stop functioning once their battery is depleted (Batsleer *et al.*, 2020). It is worth noting that RFID using active tags is sometimes referred to as radio telemetry. It is much rarer, although not unheard of, for passive RFID to be referred to as such. Radio Frequency Identification systems can also make use of either fixed or mobile antennas. Active tags are exclusively used with mobile antennas, while passive tags may be used with either depending on the research question and technical requirements of a study. There are thus three broad categories of RFID system: active tags with mobile antennas, passive tags with mobile antennas, and passive tags with fixed antennas. In entomological studies active tags can achieve read ranges hundreds of meters long, passive tags with mobile antennas can have read ranges of tens of centimetres, while the smaller passive tags paired with fixed antennas typically have read ranges of < 3 cm (Batsleer *et al.*, 2020).

1.5.2. Application in vertebrate ecology

In terms of scope, the largest active RFID studies occur in marine mammals, using tags powerful enough to be detected from space. The WhaleWatch project is a good example, using satellite-based RFID detection on blue whales (*Balaenoptera musculus*, L.) to track seasonal changes in their migration and habitat use. Another common application of active RFID in vertebrate ecology is the use of RFID collars to track large mammals such as the Iberian lynx (*Lynx pardinus*, Temminck) or wolf (*Canis lupus*, L.) during conservation efforts (Mech & Barber, 2002; Rueda *et al.*, 2021).

Passive RFID tags with a mobile antenna have been used to study the movement of salamanders (*Ambystoma annulatum,* Cope, and *A. maculatum*, Shaw) by Ousterhout and Burkhart (2017) and Ousterhout and Semlitsch (2018). They confined the tagged amphibians to mesocosms in the field which allowed direct comparisons between different environments. Confining the tagged salamanders also gave the researchers more easily searchable areas of natural habitat, allowing them to use smaller passive tags rather than active radio telemetry tags, which was important given the small size of their study species.

Passive RFID with fixed place antennas has been used in vertebrate ecology too. This has been carried out on *Gasterosteus aculeatus* (L.; three-spined sticklebacks) in artificial pond networks to compare the dispersal behaviour of different populations. However, most RFID work with fixed antennas in vertebrates has been carried out on birds. One of the early works pioneering this approach was the study of Kerry, Clarke and Else (1993) on Adélie penguins (*Pygoscelis adeliae***,** Hombron and Jacquinot). They combined RFID tagging with a weighbridge at narrow entrances to breeding colonies, to track the timing of foraging as well as weight changes in relation to foraging and food provisioning for chicks. Fixed antennas incorporated in artificial feeders is another common tactic for studying the foraging of birds (Brewer *et al.*, 2011; Hou, Verdirame & Welch, 2015; Siekiera *et al.*, 2020). One of the most complex fixed-antenna passive RFID systems has been used to study the common waxbill (*Estrilda astrild*, L.; Beltrão *et al.*, 2021, 2022; Beltrão, Gomes & Cardoso, 2022, 2023; Gomes *et al.*, 2022; Beltrão, 2023; Gomes, Boogert & Cardoso, 2023; Saldanha *et al.*, 2024). Radio frequency identification-enabled aviaries were used to study the social interactions of captive waxbills while foraging, generating powerful social network data based on which birds displaced each other at feeders.

1.5.3. Application in invertebrate ecology

In entomology, active tags in combination with mobile antennas have been used to track the dispersal of insects across distances in the order of kilometres, often using tags small enough to allow flight (Lorch & Gwynne, 2000; Hedin & Ranius, 2002; Beaudoin-Ollivier *et al.*, 2003; Hedin *et al.*, 2008; Wikelski *et al.*, 2010; Chiari *et al.*, 2013; McCullough, 2013; Liégeois, Tixier & Beaudoin-Ollivier, 2016; Růžičková & Veselý, 2016, 2018; Kennedy *et al.*, 2018; Thomaes *et al.*, 2018; Kim *et al.*, 2019; Al Ansi, Aldryhim & Al Janobi, 2020). Often the direction, time, and distance of dispersal are incorporated with observations of the microhabitat occupied when tagged insects are relocated. Very similar studies can be carried out using passive RFID tags and mobile antenna, albeit at smaller scales (Vinatier *et al.*, 2010; Pope *et al.*, 2013, 2015). Typically, this method is not applied to flying insects.

Passive RFID using fixed antenna in entomology is most commonly carried out on honeybees (*Apis mellifera*, L.) or bumble bees (*Bombus* spp.; Batsleer *et al.*, 2020). These provide ideal subjects for fixed antenna tracking because they are eusocial, have good navigational ability, readily occupy artificial shelters, and do not frequently change their nesting location (Osborne *et al.*, 2013; Kheradmand & Nieh, 2019). These traits mean that large numbers of tagged insects can be released into a hive designed to force them to enter/exit through the read range of the RFID antenna, and then reliably monitored for multiple excursions. Studies have been conducted using similar designs in the field and mesocosms, with an antenna or directional reader placed at the entrance/exit (Molet *et al.*, 2008; Stelzer, Stanewsky & Chittka, 2010; Stelzer & Chittka, 2010; Schneider *et al.*, 2012; Tenczar *et al.*, 2014; Russell, 2016; Thompson *et al.*, 2016; Nunes-Silva *et al.*, 2019). An example of a typical study is that carried out by Stanley *et al.* (2016), who investigated the changes to honeybee foraging in response to thiamethoxam. They found the pesticide-exposed bees spent longer on foraging trips, but interestingly, showed better homing ability than control bees.

1.5.4. Effects of tagging on insects

In their review, Batsleer *et al.* (2020) highlighted that many entomological studies do not adequately test tagging procedures for their effect on the study species. Studies which have tested the effect of tag weight on the ability of insects to fly have sometimes shown complete impediment of take-off (Boiteau & Colpitts, 2001; Hamidi *et al.*, 2017; Barlow, O'Neill & Pavlik, 2019; Al Ansi, Aldryhim & Al Janobi, 2020). More subtle effects, such as reductions in the speed of movement, vertical climbing ability, or increases in resting times, have also been reported (Boiteau *et al.*, 2010; Hagen, Wikelski & Kissling, 2011; Kaláb *et al.,* 2021). In addition to tag weight, the glues used for the attachment of RFID tags can be damaging. Cyanoacrylate glues, which are the most commonly used in entomology, have been shown to increase mortality and/or inhibit mobility in multiple different species, although others are reported to be unaffected (Boiteau *et al.*, 2009; Pope *et al.*, 2015; Switzer & Combes, 2016; Kirkpatrick *et al.,* 2019; Toppa *et al.*, 2020). Toppa *et al.* (2020) is a particularly thorough study, being one of very few to test both glue-alone and glue-with-tag treatments. They showed additive detrimental effects from the weight of tags and the toxicity of cyanoacrylate glue, including physical damage to flight muscles. Behavioural research is clearly of most value when the method of study does not alter the behaviour of the study species. Minimising the effects of tagging on insects is therefore important so that the conclusions drawn from tagging-based studies are as applicable to natural conditions as possible.

1.5.5. Comparisons to other remote monitoring techniques

Video monitoring is a remote monitoring technology which can be very similar to RFID, especially the application of RFID as used by Dyer *et al.* (2023) and Terlau *et al.* (2023). Video monitoring can be relatively simple, such as positioning a camera to record a sessile species (Orpet, Crowder & Jones, 2019a). In other cases, software tracking such as EthoVision® (Noldus Information Technology BV, Wageningen, Netherlands) can be used to not only record study species in an arena, but to autonomously generate analytical statistics on the movement of individuals. This type of tracking can also be supplemented with the attachment of non-electronic tags to aid software in tracking the insects (Crall *et al.*, 2018; Kaláb *et al.*, 2021). A particularly exciting application of this approach is the use of QR codes and video monitoring to generate social network information from ants (Stroeymeyt *et al.*, 2018). Without software to parse video data, it can be very time consuming to process, and in terms of storage, the data files generated will be much larger than equivalent RFID studies. Also, unless individuals are visually distinct, video monitoring may not allow unique identification. However, a video captures a much greater volume of information on the behaviour of the study species, while an RFID system merely shows where an animal was at specific times. Another advantage is that video monitoring does not necessarily involve attaching a tag to insects.

Harmonic radar is frequently discussed alongside RFID (Reynolds & Riley, 2002). This similarly involves the attachment of tags, although harmonic radar tags have a large metal loop or wire (O’Neal *et al.*, 2004). Through triangulation, the real-time flight paths of insects can be assessed using harmonic radar; however, terrain can interfere with this technique to a greater extent than RFID (Capaldi *et al.*, 2000; Batsleer *et al.*, 2020). Additionally, the design of the tags makes them easy to entangle on the environment, disrupting movement (Boiteau *et al.*, 2011). Harmonic radar tags also cannot be distinguished from one another, so only a small number of individuals can be monitored at once.

Finally, LIDAR is more similar to harmonic radar than RFID, in that it allows the real-time tracking of insects in flight. Unlike RFID and harmonic radar, LIDAR does not require the tagging of study species, meaning insects are left relatively undisturbed by this technique. This system detects the periodic light scattering from insect wings while they flap (Brydegaard *et al.*, 2021). By monitoring the frequency of these, it can be possible to distinguish between different species if their wingbeat frequencies are sufficiently different (Andersson, 2018; Song *et al.*, 2020). However, identification of individuals cannot be achieved. Another drawback of LIDAR is that while it can be operated during daylight, it tends to work best in the dark (Jansson *et al.*, 2021).

1.5.6. Radio frequency identification and *Forficula auricularia*

To the author’s knowledge, no studies have been published using RFID on *F. auricularia*. Because of the difficulty in observing *F. auricularia* during the active portion of its daily routine, a remote monitoring solution to study the foraging or shelter use of *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* within a mesocosm environment would be video monitoring. Because *F. auricularia* is nocturnal, cameras would need to operate in red light or infrared in order to observe *F. auricularia* 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 *F. auricularia* during darkness. Harmonic radar and LIDAR are both techniques for studying flying insects, and thus not particularly relevant to the study of *F. auricularia.*

1.6. Conclusions

Overall, there seem to be three main factors crucial to the success of natural control of WAA by *F. auricularia.* First, and perhaps most important, *F. auricularia* must be present in abundance. Not all *F. auricularia* present will feed on WAA, but larger populations of *F. auricularia* will lead to more complete searching of the environment and may help overcome any reduction in efficiency from alternative food sources. Second, *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* populations, in terms of both distribution and abundance. Due to their nocturnality, *F. auricularia* are difficult to observe while active in orchards, and instead a great deal of research has relied on refuge trapping. *Forficula auricularia* 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 *F. auricularia* is distributed so variably might allow growers to manage orchards to help produce a more consistent benefit from *F. auricularia* predation of WAA.

Remote monitoring using RFID has the potential to provide valuable information on *F. auricularia* 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 *F. auricularia*. This should be followed by attempts to quantify the effects of tagging on *F. auricularia*, to ensure that conclusions from tagging studies can be properly contextualised in comparison to ‘natural’ behaviour.

1.7. Aims and objectives

This research aimed to contribute to the understanding of interactions between WAA and *F. auricularia* to evaluate the potential efficacy for *F. auricularia* to be used as a natural enemy of WAA. To assess this, studies were performed on the distribution of *F. auricularia* and WAA across commercial apple orchards, to investigate the use of artificial shelters to improve *F. auricularia* abundance and to determine the viability of passive RFID tagging for the remote monitoring of *F. auricularia*.

Surveys of *F. auricularia* and WAA were conducted and molecular gut content analyses performed across commercial orchards in Kent. This was carried out to investigate factors which potentially influence the distribution of *F. auricularia* and WAA, as well as to look for evidence of *F. auricularia*’s effectiveness as a natural enemy of WAA.

Next, the impact of artificial shelters for *F. auricularia*, such as those used in refuge trapping, was investigated in an experimental orchard. The aim of this study was to ascertain if the provisioning of artificial shelters increased the abundance of *F. auricularia*, and if this in turn led to a decrease in WAA abundance.

Finally, a methodology was tested for attaching RFID tags to *F. auricularia*. This assessed the efficacy and toxicity of different glues and designing a prototype RFID-enabled mesocosm for the study of *F. auricularia* behaviour.

2. The presence of *Forficula auricularia* and *Eriosoma lanigerum* in orchards in Kent

2.1. Introduction

The woolly apple aphid (*Eriosoma lanigerum*, Hausmann; WAA) is a pest of apple (*Malus domestica*, Bork) worldwide. This species attacks the woody tissue of trees both above and below ground (Marcovitch, 1934). Toxins released in the aphids' saliva during feeding cause galling, which disrupts plant growth (Brown *et al.*, 1995; Wool, 2004). Severe galling can act as sites for secondary infection by pathogens, in particular *Neonectria ditissima*, also referred to as apple canker (Childs, 1929; Asante, Danthanarayana & Cairns, 1993; Biello *et al.*, 2021). Honeydew excreted by the WAA can also lower photosynthesis (Guerrieri & Digilio, 2008).

The ability of WAA to survive underground on the rootstock of apple trees makes effective control with insecticide sprays challenging. Organophosphates were reported to be effective, however this class of insecticide is now heavily regulated or banned in many countries (Beers, Cockfield & Fazio, 2007). In the United Kingdom (UK), Batavia® (Bayer Crop Science, Cambridge, UK; with the active ingredient spirotetramat), is currently the most commonly used insecticide applied to control WAA (Ridley *et al.*, 2024). Batavia is a two-way systemic pesticide, allowing it to effect WAA colonies on both the scion and rootstock (Nauen *et al.*, 2007; Schoevaerts *et al.*, 2011). However, Batavia is also expensive, and frequently only reduces WAA populations without eliminating them. There is, therefore, interest in improving control of WAA using natural enemies in conservation and augmentation biological control approaches.

Previous research has shown that of the natural enemies of WAA, the common European earwig (*Forficula auricularia*, L.) is particularly important (Nicholas, Spooner-Hart & Vickers, 2005; Orpet, Crowder & Jones, 2019). There are several field studies which suggest that high population densities (> 5 individuals per tree) of *F. auricularia* can provide adequate control of WAA without the use of insecticides (Mueller, Blommers & Mols, 1988; Nicholas, Spooner-Hart & Vickers, 2005; Quarrell, Corkrey & Allen, 2017). However, other studies have shown a lack of WAA control despite *F. auricularia* being present (Carroll, Walker & Hoyt, 1985; Marshall & Beers, 2021, 2022). There appear to be two main factors which influence the effectiveness of *F. auricularia* in controlling WAA. These are the population density of *F. auricularia*, and the presence of *F. auricularia* early in the growing season before WAA can become well established (Quarrell, Corkrey & Allen, 2017). Studies which have shown successful WAA control often employ augmentative releases of *F. auricularia* (Mueller, Blommers & Mols, 1988; Orpet *et al.*, 2019a; Alins *et al.*, 2023; Hanel *et al.*, 2023). In addition, recent research has suggested that *F. auricularia* releases must be continued for multiple years in order to be effective against WAA (Alins *et al.*, 2023; Hanel *et al.*, 2023). However, other studies relying on naturally occurring *F. auricularia* populations have shown control of WAA (Nicholas, Spooner-Hart & Vickers, 2005; Helsen *et al.*, 2007; Quarrell, Corkrey & Allen, 2017; discussed further below).

As well as correlation evidence based on refuge trapping or exclusion of *F. auricularia* from apple tree canopies, gut content analysis has provided direct evidence for *F. auricularia* predation of WAA in the field. While older studies have used visual inspection of the gut contents to investigate diet and demonstrated the highly polyphagous and omnivorous nature of *F. auricularia* (Lamb & Wellington, 1975; Phillips, 1981), more recent studies have used molecular gut content analysis to investigate the consumption of specific prey groups.

Romeu-Dalmau, Piñol and Agustí (2012) used a set of non-species-specific aphid primers to study the consumption of seven different aphid species in an organic citrus orchard. Orpet *et al.* (2019a) investigated *F. auricularia* consumption of WAA specifically, in four organically managed orchards, in plots where the *F. auricularia* population had been enhanced through augmentative releases.

While augmentative releases of trap-caught *F. auricularia* are one way to ensure a large population of this natural enemy in apple orchards, it is unclear if high numbers of *F. auricularia* remain once releases are stopped (Gobin *et al.*, 2007). The population dynamics of *F. auricularia*, namely the factors influencing which apple orchards naturally contain high numbers of *F. auricularia*, are poorly understood. Previous research has suggested that soil temperature may be important (Phillips, 1981). Helsen *et al.* (2007) studied *F. auricularia* and WAA populations in multiple orchards, mainly comparing Integrated Pest Management (IPM) to organic management. They showed that across both management types, higher numbers of *F. auricularia* were correlated with lower levels of WAA infestation. They also found *F. auricularia* was more abundant in organic orchards, with the other key factor affecting *F. auricularia* abundance being soil drainage. It is worth noting that Helsen *et al.* (2007) do not present any statistical analysis of their data, instead relying on summary statistics. Happe *et al.* (2018) studied the influence of the surrounding landscape on the number of *F. auricularia* in orchards. Plant species richness, and orchard cover in the surrounding landscape did not impact *F. auricularia* numbers, neither did organic management (*vs.* IPM). The only significant landscape effect they found on *F. auricularia* was that nearby woodland was associated with fewer *F. auricularia* in organic orchards in Germany in July, but this was not the case in Spain or in the same German orchards in September. *Forficula auricularia* numbers in apple orchards are highly variable across both space and time (Phillips, 1981; Burnip *et al.*, 2002; Gobin *et al.*, 2006; Gobin *et al.*, 2007 Moerkens *et al.*, 2009). To date, there is no strong explanation for what drives this variability.

As high population densities of *F. auricularia* are associated with stronger WAA control, and apple orchards can naturally have high numbers of *F. auricularia*, there is a clear incentive to identify the causes. There is also a need to investigate if apple growers can enhance the abundance of *F. auricularia* in their orchards without resorting to augmentative releases, which may be costly and time consuming. Research on the effectiveness of naturally occurring *F. auricularia* populations in controlling WAA would be advantageous to understand how to enhance control. This study aimed to survey apple orchards and investigate any orchard characteristics which were associated with populations of WAA or *F. auricularia*. In addition, gut content analysis, in combination with the survey data, was used to investigate the interactions between naturally occurring populations of *F. auricularia* and WAA.

2.2. Methods

2.2.1. 2022 Methods

2.2.1.1. 2022 Experimental design

Eleven orchards belonging to six different growers were selected. Selection was restricted to the variety Gala. Of the 11 orchards, three were organically managed, all belonging to the same grower. All other orchards were conventionally managed. A full list of the orchards used in this study, their management style, and the grower they belonged to, is in Table 2.1. Within each orchard, a random sample of 50 trees was generated using the tree row and tree number along the row as x-y coordinates in Microsoft Excel (Microsoft Office 16, v. 16.0.16130.20218). These trees were then surveyed qualitatively for the level of WAA infestation, on a scale from 0 to 3 (Table 2.2; Nicholas, Spooner-Hart & Vickers, 2005; Quarrell, Corkrey & Allen, 2017). After this, the 10 trees which scored the highest for WAA infestation were selected for inclusion in the surveys. When this involved selecting between trees with the same score, this was done randomly (Microsoft Excel). As a result of this process, the 10 trees in each orchard constitute a semi-random sample representative of the most infested trees in each orchard (110 trees total). Two rounds of surveys were completed, roughly corresponding to the months of July and September. Two rounds of molecular collections were also completed. The timing of these is discussed below, as the first of these did not coincide with the first round of surveys, while the second did. A full account of the dates of each survey and molecular collection are available in Tables A-1 and A-2. Soil penetrometer readings were taken in November and December after the surveys and molecular collections.

Table 2.1. A list of the orchards surveyed in 2022.

Orchard	Grower	Management Style	Whole/Subset	Variety	Age (Years)	Multi Row?
1	1	Conventional	Whole	Gala	12	N
2	1	Conventional	Whole	Gala	15	N
3	2	Conventional	Whole	Gala	12	N
4	3	Conventional	Subset	Gala	20	N
7	4	Conventional	Whole	Gala	22	Y
8	4	Conventional	Whole	Gala	11	Y
12	5	Conventional	Whole	Gala	16	N
13	5	Conventional	Whole	Gala	9	N
14	6	Organic	Subset	Gala	9	N
16	6	Organic	Whole	Gala	13	N
17	6	Organic	Whole	Gala	4	N

Table 2.2. Scoring criteria used to qualitatively assess the level of WAA infestation prior to the selection of trees for inclusion in the 2022 survey.

Score	Description
0	No visible WAA
1	Small colonies of less than 5 individuals present, no more than 1 or 2 medium colonies containing 5 to 15 individuals
2	Contains 3 to 7 medium colonies, and no more than 1 or 2 large colonies with more than 15 individuals
3	At least 3 large colonies, or more than 7 medium colonies, small colonies widespread

2.2.2. 2022 Monthly field measurements

2.2.2.1. *Forficula auricularia* counts

A single refuge trap was attached to the canopy of each tree. Traps were made from transparent 2 L plastic bottles (diameter = 10 cm, length = 30 cm) with the top of the bottle cut off. These contained rolls of corrugated cardboard (width = 10 cm, length = 60 cm), and were attached to each tree using gardening wire in such a way that the corrugated cardboard would be protected from the rain (Figure 2.1). The refuges were placed 50 to 150 cm above the ground, tied to the trunk of the tree, and placed so that the bottom of the refuge rested on a branch. Refuges were placed onto trees between 2022.07.11 and 2022.07.15. During each of the two surveys, the refuge trap was detached and shaken onto a plastic tray to dislodge any *F. auricularia* inside. The number of *F. auricularia* dislodged was recorded, up to a maximum of 40. If > 40 *F. auricularia* were found in a trap, this was recorded instead. As many *F. auricularia* were returned to the refuge trap as possible, with the rest being released at the base of the tree. The refuge trap was then placed back into the tree. Where refuge traps had flipped and become waterlogged, the entire refuge trap was replaced with a new one.

Figure 2.1. An artificial shelter used as a refuge trap for *F. auricularia* in 2022.

2.2.2.2. Woolly apple aphid colony counts

On each tree the number of WAA colonies were counted. 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. Colony sizes for three colonies on each tree were also measured, but this data was discarded due to the low number of occupied trees.

2.2.2.3. Other aphids

All trees were also searched for *Aphis pomi* (de Greer) (Green Apple Aphid; GAA), *Dysaphis plantaginea* (Passerini) (Rosy Apple Aphid; RAA), and *Dysaphis devecta* (Walker) (Rosy Leaf Curling Aphid; RLCA). If found, the number of aphids of that species present on the tree was counted. Rosy leaf curling aphid and RAA were distinguished by RLCA causing leaves to roll laterally (the sides of the leaf roll in towards to the central midrib) and take on a pink/red colouration, as well as RLCA having antennae shorter than the distance between its head and siphunculi. In contrast, RAA causes leaves to curl longitudinally (from the tip of the leaf to the base where it connects to the stem) without a large change in colour, and the aphids have antennae longer than the distance between its head and siphunculi. Only GAA was detected in 2022, and measurements on all three species were discarded due to lack of data.

2.2.2.4. *Forficula auricularia* sampling for molecular gut content analysis

Two rounds of molecular collections were carried out in 2022. The first was completed between 2022.08.10 and 2022.08.11, after the first round of surveys was concluded. The second round of molecular collection occurred between 2022.08.30 and 2022.09.14, concurrent with the second survey. In both rounds of molecular collections, up to 10 *F. auricularia* were removed from each refuge trap. In cases where refuges contained more than 10 individuals, the first 10 to be shaken loose from the refuge were taken, and any remaining *F. auricularia* were released at the base of the tree. All *F. auricularia* taken for molecular gut content analysis from the same tree were placed in a bag together, live, and transported back to Niab, East Malling, UK (after surveying in the case of the second round of collections). On the same day (up to approximately 8 hours since collection), each bag of *F. auricularia* was placed in a -15 °C freezer to kill them. They remained in this freezer only for the period from killing to dissection (minimum 30 mins, maximum approximately 2 hours). They were then dissected, their guts removed, and all guts from the same tree placed into a single 2 mL PCR-clean locking Eppendorf tube to create pooled samples.

The dissection procedure was as follows. Before starting dissection, all of the *F. auricularia* from a given tree were removed from the -15 °C freezer, and surface sterilised by being submerged in 70% ethanol for 1 min, then 5% bleach for 1 min. The *F. auricularia* 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 tree. A pair of forceps was used, which were also sterilised for 1 min in 5% bleach between each group of *F. auricularia*. Each *F. auricularia* was then grasped at both the cerci and head and pulled in either direction. The foregut would typically remain attached to the head and be pulled through the thorax and pronotum. Sometimes the hindgut would also remain attached, and the entire gut was removed in a single motion. However, frequently the hindgut would detach from the foregut and remain inside the abdomen and thorax. These would then be pulled apart to retrieve the hindgut. All the extracted guts from the *F. auricularia* from a given tree were placed into one 2 mL PCR-clean locking Eppendorf tube. Once all the *F. auricularia* from one day of molecular collections had been dissected, the tubes were stored in a -80 °C freezer, until they were processed for DNA extraction using a Qiagen DNeasy blood and tissue kit.

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 *F. auricularia* 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 *F. auricularia* 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, still part of step 3 on the protocol, the samples were placed into a water bath at 56 °C. They were left to incubate for 3 hours, but were removed from the water bath every 30 mins to vortex. 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 *F. auricularia* 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 *F. auricularia*. A PCR negative control was run using 4 µl of extra water in place of DNA.

2.2.3. 2022 One-time measurements

2.2.3.1. Moss, algae, and lichen scores

The first round of surveys included a qualitative assessment of the abundance of moss, lichen, and algae present in the orchards. Since no lichen was found, this measure was discarded. The quantity of moss and algae was rated on a scale from 0 to 3. The criteria for these scales are given in Table 2.3 along with example images (Figure 2.2).

Table 2.3. Scoring criteria used to assign a qualitative moss score and algae score to each tree surveyed in 2022. Note that moss score 3 was assigned to only one tree.

Moss Score	Description	Algae Score	Description
0	Absent	0	Absent
1	Small patches of moss present in the tree beds, but with the majority of ground cover taken up by bare soil, grass, or other plants.	1	Small amounts of algae only present on burrs, cankers, or creases in the tree
2	Large patches of moss take up approximately 50% of the surface area of the bed or more, in 1 m^2 around the tree	2	Large patches of algae more common and may appear on smooth patches of tree.
3	Moss growing on the tree itself	3	More than 50% of the tree's surface is green with algae. The algae are thick enough to form their own texture

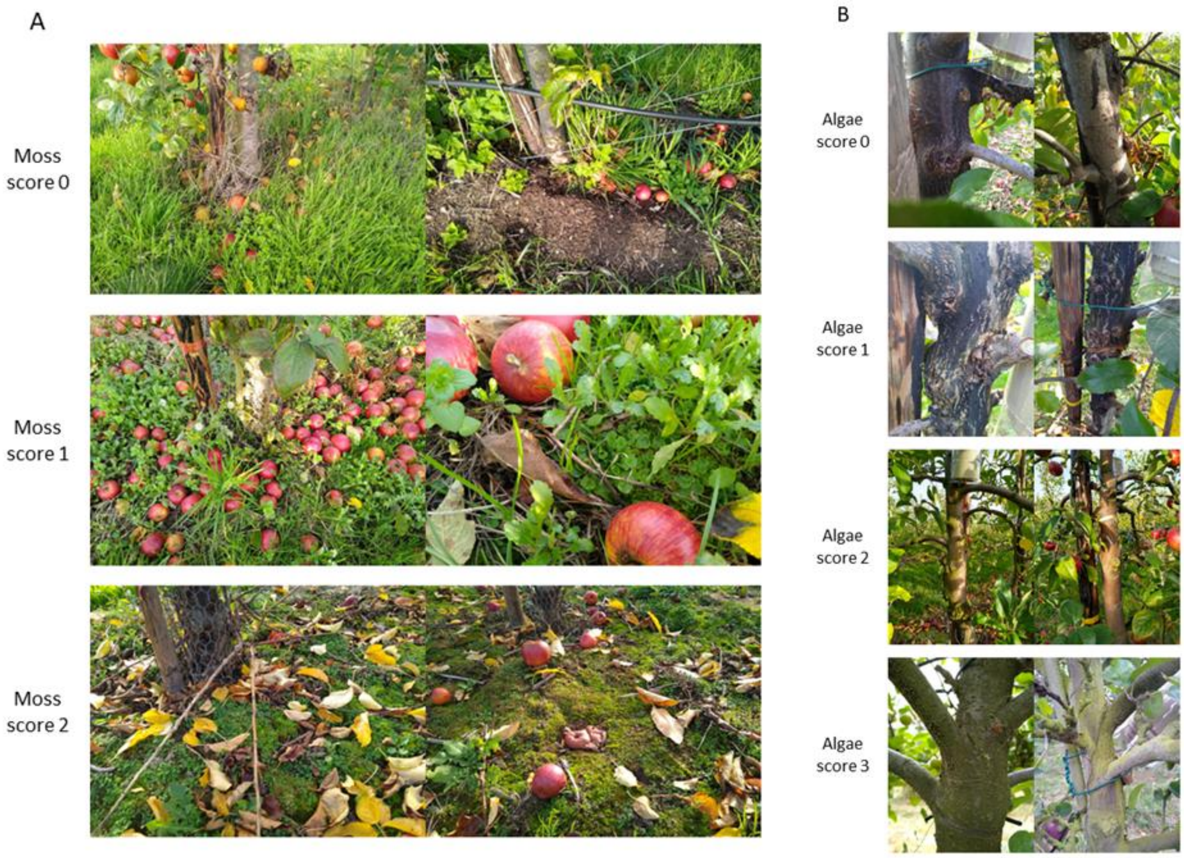

Figure 2.2. Example images demonstrating each level of the scoring criteria used to rate the abundance of moss (A) and algae (B) on or underneath each tree in 2022.

2.2.3.2. Soil firmness

Soil firmness was measured using a soil penetrometer (Solutions for Research Ltd., Bedfordshire, UK). These were corrected for moisture content using a MO750 model soil moisture meter (Extech Instruments Corp., New Hampshire, USA). Soil firmness and moisture readings were taken as close as possible to the base of each tree, in the row bed. Where the probe of the soil penetrometer was obstructed by roots or stones in the ground, the penetrometer was moved a short distance, so that it was still in the row bed but further away from the base of the tree, before repeating the measurement. The first soil penetrometer measurements were taken on 2022.11.18 and the last on 2022.12.09. The soil penetrometer measures the force required to drive it into the ground every 2.5 cm up to a maximum depth of 55 cm (22 readings per complete probe). The measurements from the penetrometer were converted from kg/cm^2 values to MPa values, corrected for the mean moisture content of the orchard, and then a mean MPa force for each orchard at each depth was calculated and zeroed, giving a force-depth profile for each orchard.

2.2.4. 2023 Methods

2.2.4.1. 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 as in 2022. 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 2.4. 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 *F. auricularia* 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 2.4. A list of orchards surveyed in 2023. Soil types were taken from the Soilscapes 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 *F. auricularia* 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.

2.2.5. 2023 Monthly field measurements

2.2.5.1. 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).

2.2.5.2. *Forficula auricularia* 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 *F. auricularia*. 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 *F. auricularia* 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. Figure 2.3 shows Wignests placed in-situ. The number of *F. auricularia* 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 *F. auricularia*. The time of sampling was also recorded. All *F. auricularia* were then released at the base of the tree and the Wignests repositioned on the tree.

Figure 2.3. Two Wignests used as refuge traps to monitor *F. auricularia* presence and abundance in 2023.

2.2.5.3. 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.

2.2.5.4. 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.

2.2.5.5. 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.

2.2.5.6. *Forficula auricularia* molecular collections

The collection of *F. auricularia* for molecular gut content analysis was carried out in the weeks after the *F. auricularia* 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 *F. auricularia* count from the survey, and selecting every second orchard for inclusion (*e.g.* the orchard with the most *F. auricularia*, the orchard with the 3rd most *F. auricularia*, the orchard with the 5th most *F. auricularia*, *etc*.). The 10 orchards selected this way were visited early in the morning, and *F. auricularia* were collected for molecular gut content analysis. Five of the 10 trees surveyed before were randomly selected, and up to 10 *F. auricularia* from each of these five trees were taken from the Wignests for molecular gut content analysis. The first 10 *F. auricularia* to be shaken loose from the Wignests were taken; any extra *F. auricularia* loosened were released at the base of the tree. The *F. auricularia* taken for sampling were replaced by an equivalent number of *F. auricularia* released at the base of the tree, to minimize the effect on future surveys and molecular collections. Replacement *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* 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 of the *F. auricularia* from a given tree were removed from the -80 °C freezer, and surfaced sterilised as in 2022. The *F. auricularia* 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 *F. auricularia* 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 same protocol for DNA extraction was carried out as in 2022, with the following change. 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.

The PCR analysis was carried out using the same thermocycler settings, primers, and gel electrophoresis procedures as in 2022. 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 *F. auricularia* 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.

2.2.6. 2023 One-time measurements

2.2.6.1. Pitfall trapping

Pitfall trapping was carried out in October, in a subset of eight orchards. To select orchards for pitfall trapping, the total *F. auricularia* count across all three surveys was used: the two conventional orchards with the highest count and the two conventional orchards with the lowest count were selected and the same was performed for organic orchards. Within each selected orchard, five of the 10 trees monitored during the 2023 surveys were randomly selected. Pitfall traps were placed one row along from the selected trees, and then 1.5 trees along from the selected trees (*e.g.* if original tree = T58 then the pitfall trap location = U59.5). These rules for pitfall trap placement were occasionally flipped to ensure that no pitfall traps were placed outside of the orchard, and there was a minimum of three trees between pitfall traps placed in the same row. A full list of the selected trees and pitfall trap locations is available in Table A.5. The pitfall traps were created from 400 mL plastic cups with a base diameter of 54 mm, a top diameter of 95 mm, and a height of 107 mm (AIOS Drinkware, Avenue Group Ltd., Colnbrook, UK). The pitfall traps were placed so that the top of the trap was flush with the ground, in line with the tree row, and equidistant from the two adjacent trees. Each trap was filled with 250 mL of 70% ethanol. A wire mesh with aperture size 15 mm was placed over the top of each pitfall trap, flush with the ground. A lid was placed above the pitfall trap with approximately 1.5 cm of clearance from the ground. Three 50 mm nails (Kingfisher International Products Ltd., London, UK) were driven through the lid and into the ground to suspend the lid and keep it in place. Figure 2.4 shows a pitfall trap in-situ. The pitfall traps were left for between seven and 10 days in each orchard, after which they were removed, and the number and sex of any *F. auricularia* captured were recorded.

Figure 2.4. Images of a pitfall trap with and without the wire mesh and lid covering, used to monitor *F. auricularia* abundance in 2023.

2.2.6.2. Soil type

The soil type for each orchard's location was taken from the Soilscapes 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".

2.2.7. Statistical analysis

Statistical analyses of both the 2022 and 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, 2015), glmmTMB (Brooks *et al.,* 2025), 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 *F. auricularia*. 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. For both years, 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 in both years. Whether an orchard was managed organically or conventionally (referred to as management style) was treated as categorical for both 2022 and 2023. The capped *F. auricularia* counts from 2022, and the uncapped *F. auricularia* counts from 2023 (from refuge trapping in both years), were converted to binary presence or absence variables due to the high number of zeros. The WAA colony counts from 2022 and the WAA estimated percentage infestations from 2023 were similarly converted into binary presence or absence variables due to the high number of zeros. In 2022 the moss and algae scores were treated as categorical, while lichen score was discarded. In 2022 orchard age was initially treated as numerical, but was discarded due to the volume of data being too small to support orchard age as a factor in more complex models. None of the additional aphid species (GAA, RLCA, or RAA) were detected in high enough numbers in 2022 to be included in modelling, so all were discarded. In 2023, GAA and RLCA were similarly 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 $\geq 50\%$. 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 in this chapter.

The accepted models were:

- 2022 WAA Baseline had tree within orchard within grower as nested random effects and the month of survey as a fixed effect
- 2022 WAA Assembled had tree as a random effect and month of survey and management style as fixed effects
- 2022 *F. auricularia* Baseline had tree within orchard within grower as nested random effects with no fixed effects
- 2022 *F. auricularia* Assembled had tree as a random effect, management style and WAA presence as fixed effects, with an interaction effect between management style and WAA presence
- 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, *F. auricularia* presence, RAA presence, and moss presence as fixed effects;

with interaction effects between management style and the month of survey, and management style and *F. auricularia* presence

- 2023 *F. auricularia* Baseline had tree within orchard within grower as nested random effects and the month of survey as a fixed effect
- 2023 *F. auricularia* Assembled had tree as a random effect, the month of survey, RAA presence, and bare earth abundance as fixed effects

These are discussed further below.

To analyse the soil penetrometer data across the depth profile, the corrected mean penetration resistance of each orchard was ranked at each depth. These ranks at each depth were then summed for all depths, to give each orchard an overall soil firmness score, such that a low score indicated higher mean soil firmness. These scores were then compared to the total refuge trap catch of *F. auricularia* during the 2022 surveys.

To account for the different lengths of time pitfall traps were deployed in the orchards, the total trap catch for all pitfall traps in a given orchard was divided by the number of days the traps were present to create the days-standardised pitfall trap catch of the orchard. These days-standardised pitfall trap catches were then compared to the total refuge trap catch of *F. auricularia* during the 2023 surveys.

2.3. Results

2.3.1. Summary of survey data

The abundance of *F. auricularia* and WAA at the orchard level were both highly variable, with large differences between orchards, between the same orchard on different surveys, and between years (Table 2.5 and Table 2.6). In particular, total *F. auricularia* counts in 2023 tended to be much higher than in 2022. An average of 3.2 (± 74.4; standard deviation) *F. auricularia* were caught per pseudo-tree in 2022, while 17.9 (± 224.5) were caught in 2023. The WAA abundance is less easy to compare between years due to the different survey methods, however, the proportion of pseudo-trees infested with WAA is available for both years. In 2022 74.5% of pseudo-trees contained WAA, in 2023, only 26.7% of pseudo-trees contained WAA.

Table 2.5. The total number of *F. auricularia* (earwigs) and WAA colonies found on ten trees per orchard during each survey in 2022. Note that during the September survey of Orchard 12, five trees contained >40 *F. auricularia*. For these trees the *F. auricularia* count was marked as “>40” rather than as an exact count.

Orchard	Grower	Management style	Variety	Total earwig count		Total WAA colony count	
				July	September	July	September
1	1	Conventional	Gala	7	2	0	0
2	1	Conventional	Gala	5	48	0	0
3	2	Conventional	Gala	0	0	93	10
4	3	Conventional	Gala	20	18	0	0
7	4	Conventional	Gala	3	27	94	6
8	4	Conventional	Gala	0	0	58	9
12	5	Conventional	Gala	155	>329	0	0
13	5	Conventional	Gala	23	35	0	0
14	6	Organic	Gala	2	15	209	30
16	6	Organic	Gala	0	2	407	526
17	6	Organic	Gala	0	3	5	2

Table 2.6. The total number of *F. auricularia* (earwigs), WAA-infested trees, and RAA-infested shoots, found on/among ten trees per orchard during each survey in 2023.

Orchard	Grower	Management style	Variety	Used last year?	Total earwig count			WAA-infested trees			Total RAA-infested shoots		
					July	August	September	July	August	September	July	August	September
1	1	Conventional	Gala	Y	129	348	57	1	0	0	0	0	0
3	2	Conventional	Gala	Y	1	3	0	1	0	0	9	4	4
4	3	Conventional	Gala	Y	195	254	133	2	1	0	0	0	0
5	3	Conventional	Braeburn	N	259	269	177	0	0	0	0	0	0
6	3	Conventional	Braeburn	N	259	335	196	0	0	0	0	0	0
9	4	Conventional	Braeburn	N	608	594	275	3	0	0	0	0	0
10	4	Conventional	Braeburn	N	0	0	0	8	4	1	34	22	17
11	4	Conventional	Braeburn	N	6	3	6	9	4	5	9	9	5
12	5	Conventional	Gala	Y	809	693	441	1	0	0	0	0	0
13	5	Conventional	Gala	Y	224	473	640	1	0	0	0	0	0
14	6	Organic	Gala	Y	13	11	8	0	0	3	0	0	0
15	6	Organic	Braeburn	N	39	14	6	0	1	5	0	0	0
16	6	Organic	Gala	Y	71	79	28	10	10	10	0	0	0
18	7	Organic	Gala	N	48	175	86	4	3	9	31	23	15
19	7	Organic	Gala	N	2	24	37	6	2	7	67	45	43
20	8	Organic	Spartan	N	143	501	279	3	0	0	5	3	3
21	9	Organic	Gala	N	63	78	56	9	6	6	0	0	0
22	9	Organic	Gala	N	2	18	16	3	3	2	7	8	0
23	9	Organic	Gala	N	1	12	25	6	3	2	12	12	0
24	10	Organic	Gala	N	397	899	217	1	1	4	38	36	25

2.3.2. 2022 Results

The 2022 WAA Baseline model (Table 2.7) consisted of tree within orchard within grower as nested random effects, with survey as the only fixed effect. This model had an AIC of 115.9. The 2022 WAA Assembled model (Table 2.8) had tree as a random intercept, and survey and management style as fixed effects. The AIC of the model was 168.3. *Forficula auricularia* presence, moss score, and algae score were all excluded from the model. There were WAA present in more trees in July than September (Figure 2.5). There were more WAA-occupied trees in organic orchards than conventional orchards (Figure 2.6).

Table 2.7. A model for the presence or absence of WAA from 220 pseudo-trees (n = 110 trees, 2 surveys). AIC = Akaike Information Criterion. DF = Degrees of Freedom. Std. = Standard.

2022 WAA Baseline			
AIC	115.9		
Deviance	105.9		
DF residuals	215		
Random Effects			
Name	Type	Variance	Std. deviation
Tree	Intercept	7.528E-08	0.0002744
Orchard	Intercept	14.91	3.861
Grower	Intercept	117.2	10.83
Fixed Effects			
Name	Estimate	Std. error	*p* value
Intercept	-8.5455	3.9767	< 0.05
Survey 2	-3.405	0.8006	< 0.001

Table 2.8. A model for the presence or absence of WAA from 220 pseudo-trees (n = 110 trees, 2 surveys). AIC = Akaike Information Criterion. DF = Degrees of Freedom. Std. = Standard.

2022 WAA Assembled			
AIC	168.3		
Deviance	160.3		
DF residuals	216		
Random Effects			
Name	Type	Variance	Std. deviation
Tree	Intercept	1483	38.52
Fixed Effects			
Name	Estimate	Std. error	*p* value
Intercept	-10.48	1.431	< 0.001
Survey 2	-11.516	1.567	< 0.001
Organic	32.431	3.813	< 0.001

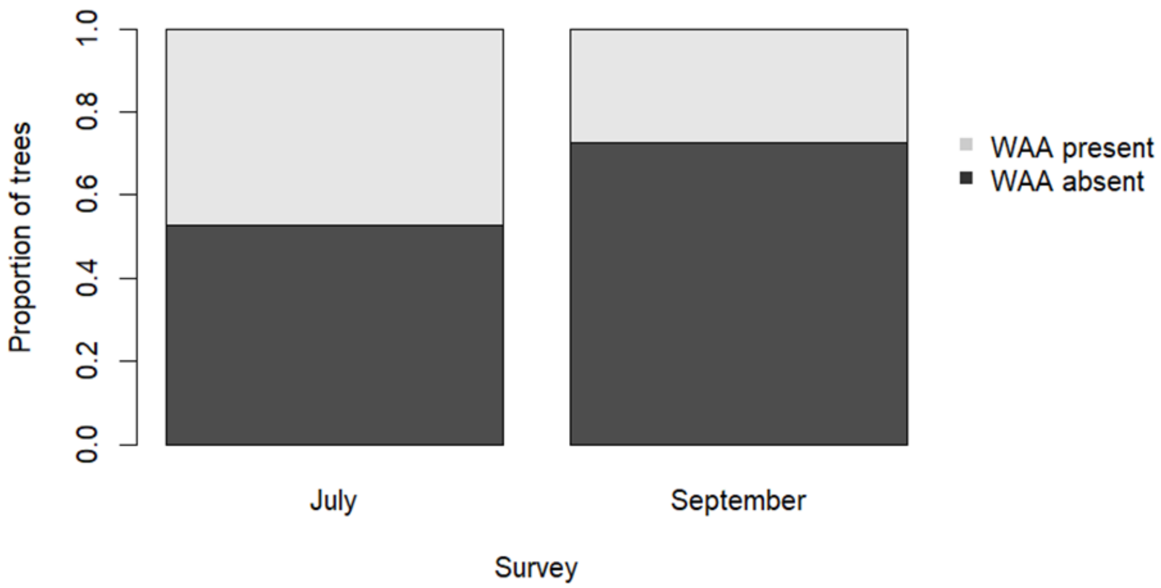

Figure 2.5. A bar chart showing the proportion of trees containing WAA from 11 orchards (N = 110 trees) surveyed twice in 2022.

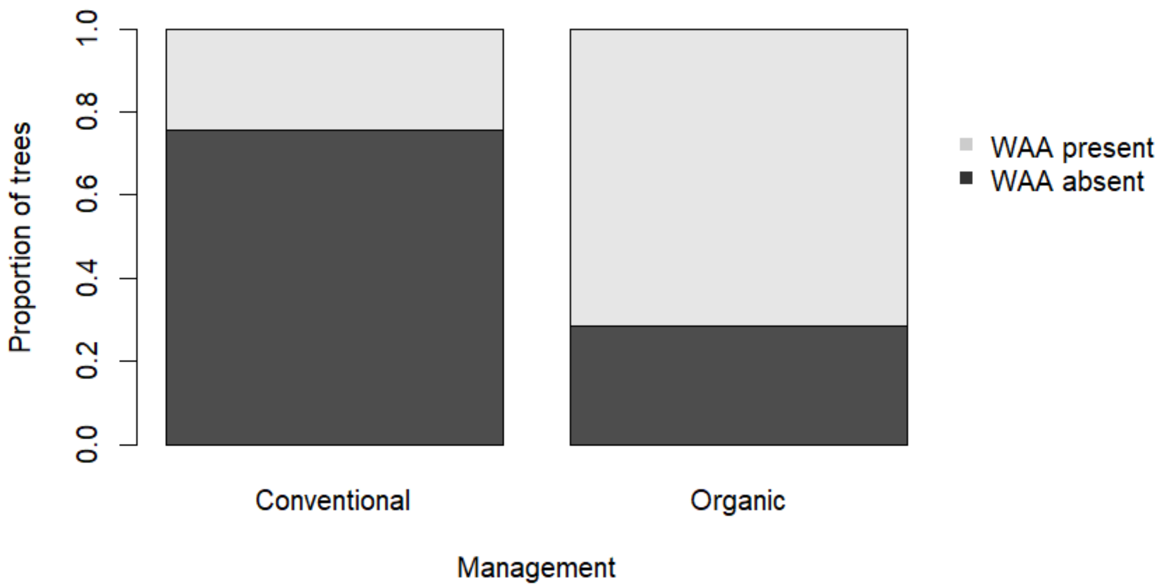

Figure 2.6. A bar chart showing the number of trees containing WAA in 160 conventionally managed pseudo-trees (*n* = 80 trees), and 60 organically managed pseudo-trees (*n* = 30 trees). Data were collected in 2022.

The 2022 *F. auricularia* Baseline model (Table 2.9) consisted of tree within orchard within grower as nested random intercepts, with no fixed effects. This model's AIC was 209.1. The 2022 *F. auricularia* Assembled model (Table 2.10) consisted of tree as a random effect, with management style, WAA presence, and their interaction, as fixed effects. The AIC of this model was 239.2. Survey and algae score were excluded from the model. Moss score was also excluded from the model, although when included as a fixed effect, Moss score 2 (large patches of moss in the row bed) shows as significant ($p < 0.05$), with an estimated effect size of -2.3814 ±0.9686 (± standard error). This indicated trees with large patches of moss in the row bed were less likely to contain WAA. Moss score was excluded despite this because Moss score 1 (small patches of moss in the row bed) was not significant ($p = 0.205$), the proportion of trees occupied by *F. auricularia* at Moss score 2 was similar to Moss score 0 (Figure 2.7), and the proportion of trees occupied by *F. auricularia* shows no clear pattern with increasing moss score from 0 to 2 (Figure 2.7). Moss score 3 (moss growing on the tree) was represented by just two trees, and so was not taken into consideration due to inadequate sample size. Figure 2.8 shows that fewer organic trees were occupied by *F. auricularia* than conventional trees, while Figure 2.9 shows that a tree was less likely to be occupied by *F. auricularia* if occupied by WAA. There was an interaction between these two effects (Figure 2.10). The line for organic trees suggests the probability of WAA infestation is similar for organic trees regardless of *F. auricularia* presence. However, for conventional trees, it is less likely to find WAA on a tree if at least one *F. auricularia* is present.

Table 2.9. A model for the presence or absence of *F. auricularia* from 220 pseudo-trees (n = 110 trees, 2 surveys). AIC = Akaike Information Criterion. DF = Degrees of Freedom. Std. = Standard.

2022 *F. auricularia* Baseline			
AIC	209.1		
Deviance	201.1		
DF residuals	216		
Random Effects			
Name	Type	Variance	Std. deviation
Tree	Intercept	1.666E-08	0.0001291
Orchard	Intercept	2.497	1.5802525
Grower	Intercept	3.614	1.9009498
Fixed Effects			
Name	Estimate	Std. error	*p* value
Intercept	-0.9527	0.9832	0.333

Table 2.10. A model for the presence or absence of *F. auricularia* from 220 pseudo-trees (n = 110 trees, 2 surveys). AIC = Akaike Information Criterion. DF = Degrees of Freedom. Std. = Standard.

2022 *F. auricularia* Assembled			
AIC	239.2		
Deviance	229.2		
DF residuals	215		
	Random Effects		
Name	Type	Variance	Std. deviation
Tree	Intercept	1.392	1.18
	Fixed Effects		
Name	Estimate	Std. error	*p* value
Intercept	0.3577	0.258	0.166
Organic	-2.8787	1.0063	< 0.01
WAA present	-3.2578	0.8105	< 0.001
Organic * WAA present	3.4881	1.3199	< 0.01

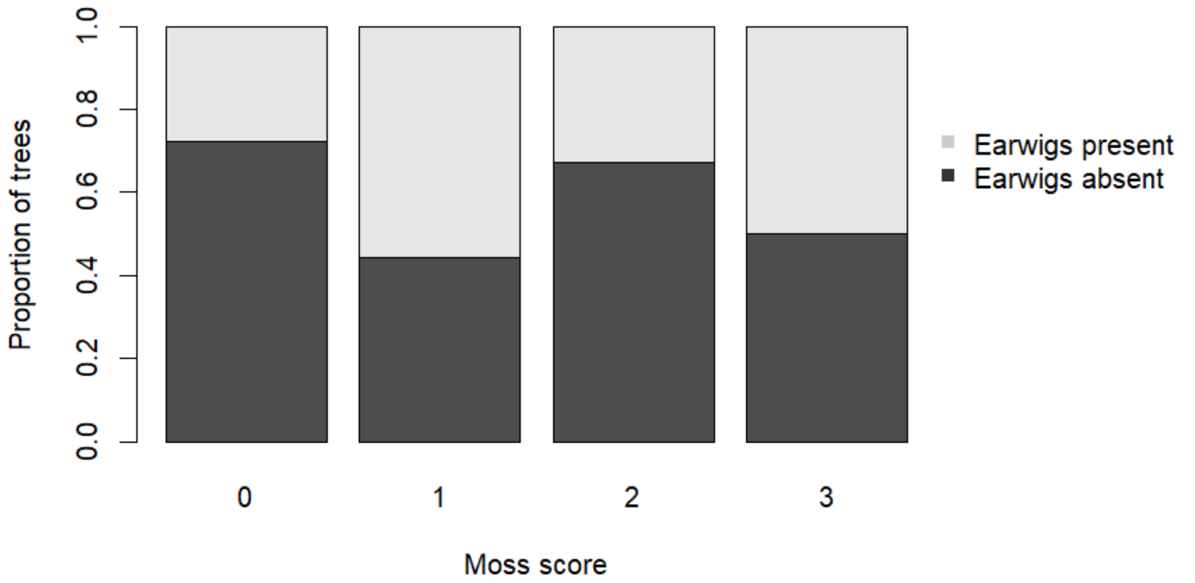

Figure 2.7. The proportion of pseudo-trees containing *F. auricularia* with different qualitative Moss scores. *n* 0 = 76 pseudo-trees (38 trees). *n* 1 = 54 pseudo-trees (27 trees). *n* 2 = 88 pseudo-trees (44 trees). *n* 3 = 2 pseudo-trees (1 trees). Data were collected in 2022.

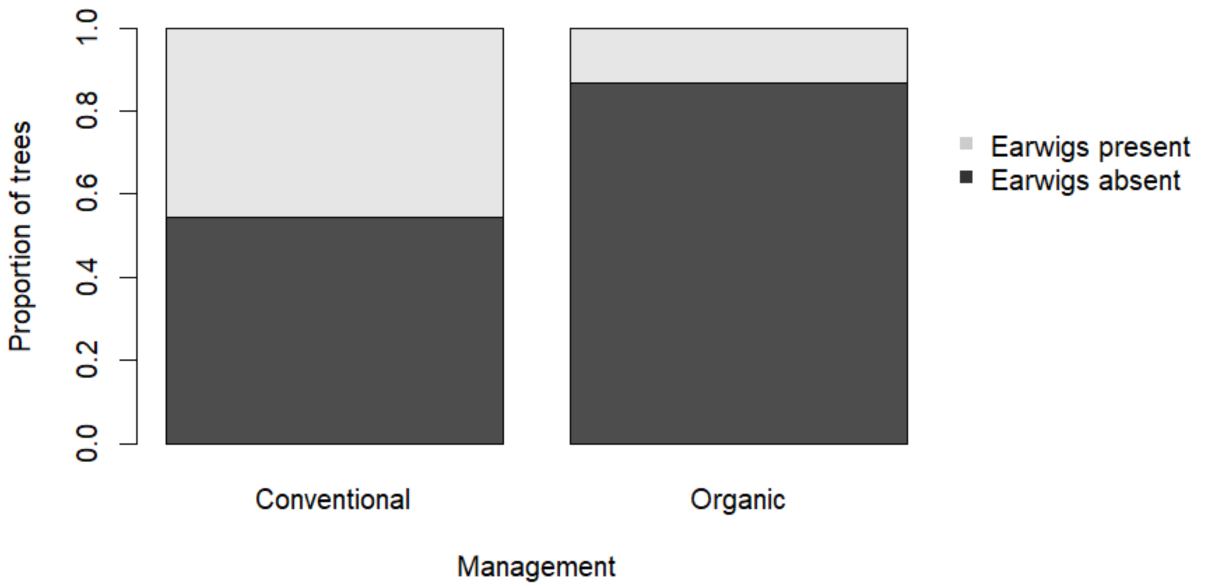

Figure 2.8. A bar chart showing the number of trees containing *F. auricularia* in 160 conventionally managed pseudo-trees (*n* = 80 trees), and 60 organically managed pseudo-trees (*n* = 30 trees). Data were collected in 2022.

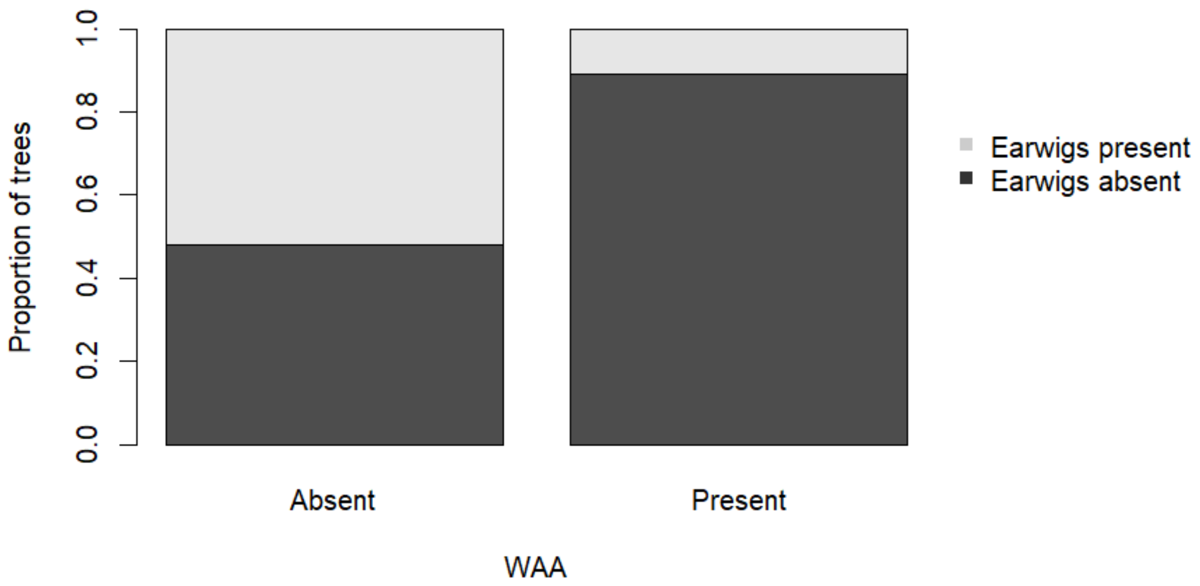

Figure 2.9. A bar chart showing the proportion of pseudo-trees containing *F. auricularia* on which WAA was Absent (*n* = 138 pseudo-trees) or Present (*n* = 82 pseudo-trees). Data were collected in 2022.

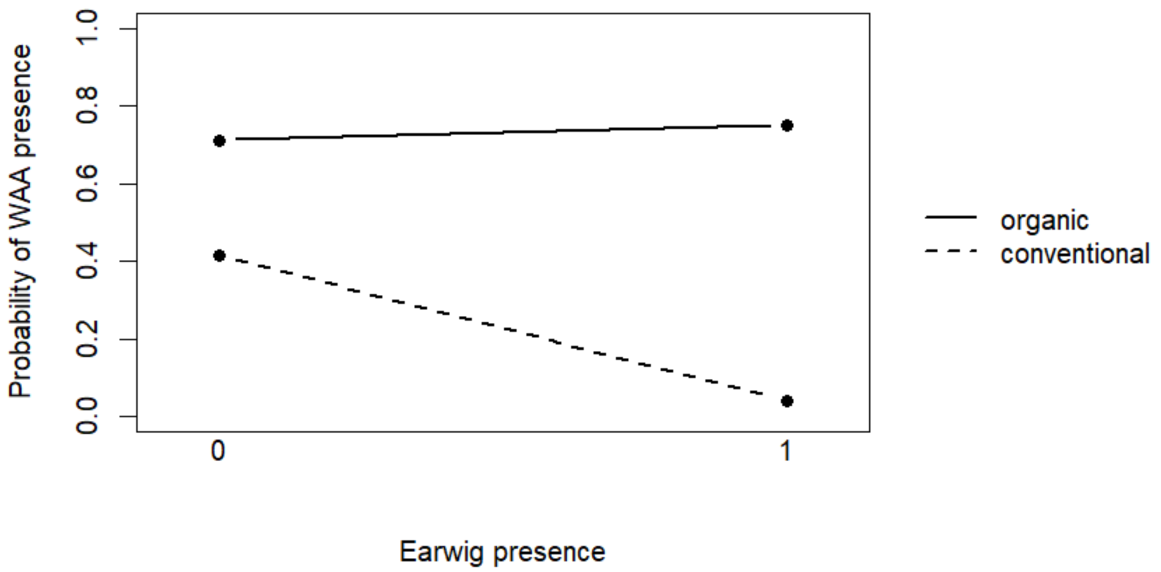

Figure 2.10. An interaction plot showing the effect of *F. auricularia* (earwig) presence (0 = Absent, 1 = Present) and management style on the probability of finding WAA in a tree. *n* conventional *F. auricularia* absent = 87 pseudo-trees. *n* conventional *F. auricularia* present = 73 pseudo-trees. *n* organic *F. auricularia* absent = 52 pseudo-trees. *n* organic *F. auricularia* present = 8 pseudo-trees. Data were collected in 2022.

The soil firmness scores showed no clear pattern with total *F. auricularia* refuge trap catch. In addition, the soil firmness profiles (Figure A-1) showed a high degree of overlap, especially at depths closer to the surface.

For the molecular gut content analysis, 370 *F. auricularia* were collected and pooled into 77 samples (each corresponding to a tree on a given survey). Of these 77 samples, five were positive, or 6.5%. Three of these positives were for single *F. auricularia*, while two came from pooled samples with 10 *F. auricularia*. This means these positives indicate aphid feeding being detected in anywhere from 5 to 23 *F. auricularia*. Given the results of the specificity test completed on *R. padi* (discussed further in the 2023 results section), it is impossible to say how many of these five positive samples are from *F. auricularia* consumption of WAA without further sequencing. All the positive samples were collected in the second round of molecular collections. Four of the five samples, including both pooled samples containing 10 *F. auricularia*, were from conventionally managed trees, while one sample, consisting of one *F. auricularia*, was from an organically managed tree.

2.3.3. 2023 Results

The 2023 WAA Baseline model (Table 2.11) 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 2.12) had tree as the only random effect. Survey, management style, earwig presence, RAA, and moss presence were all 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 2.11). Woolly apple aphid was less likely to be found on trees where moss cover was present in the row bed (Figure 2.12). Figures 2.13 and 2.14 show the individual effects of management style and *F. auricularia* presence on WAA presence. More trees were occupied by WAA in organic orchards, and fewer trees were occupied by WAA when *F. auricularia* were present. However, Figure 2.15 shows the interaction between these two factors. When *F. auricularia* were absent, trees in conventionally managed orchards had a slightly lower probability of containing WAA than organic trees. But, when *F. auricularia* 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 *F. auricularia*. Figure 2.16 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 2.17).

Table 2.11. 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	*p* 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 2.12. 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
F. auricularia 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 * *F. auricularia* present	3.0682	0.8611	< 0.001

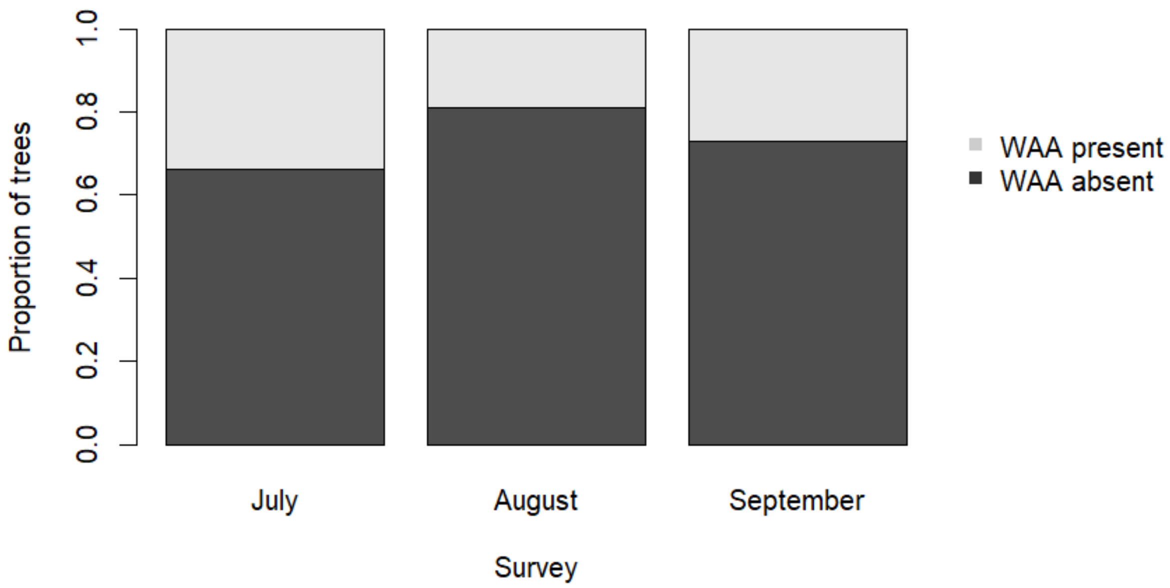

Figure 2.11. A bar chart showing the proportion of 200 trees containing WAA during three surveys conducted in 2023.

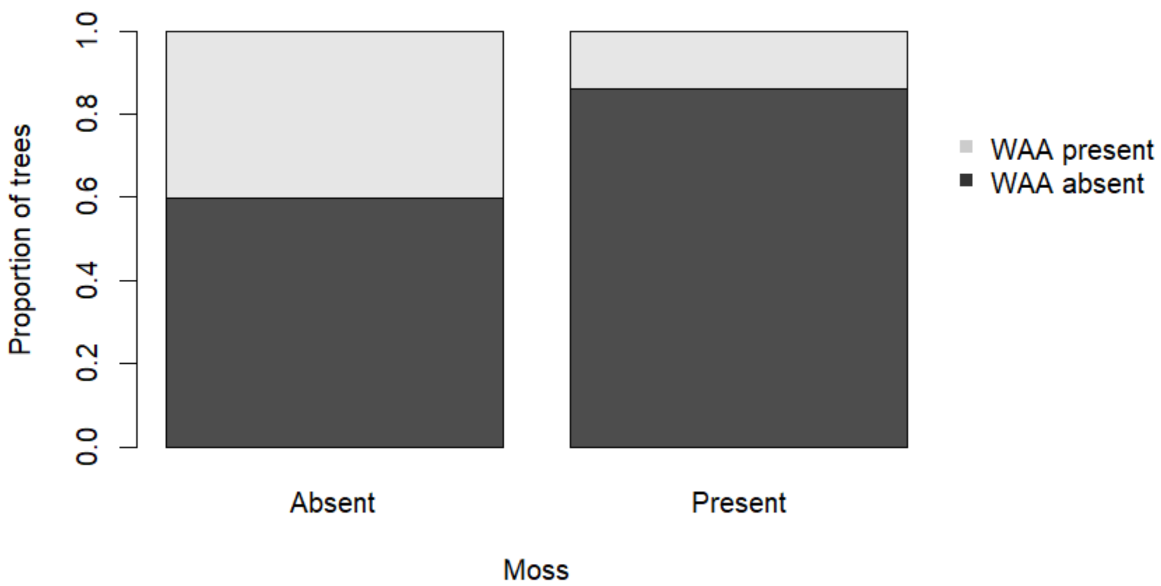

Figure 2.12. A bar chart showing the proportion of pseudo-trees containing WAA where moss was either absent (*n* = 290 pseudo-trees) or present (*n* = 310 pseudo-trees) from the row bed. Data were collected in 2023.

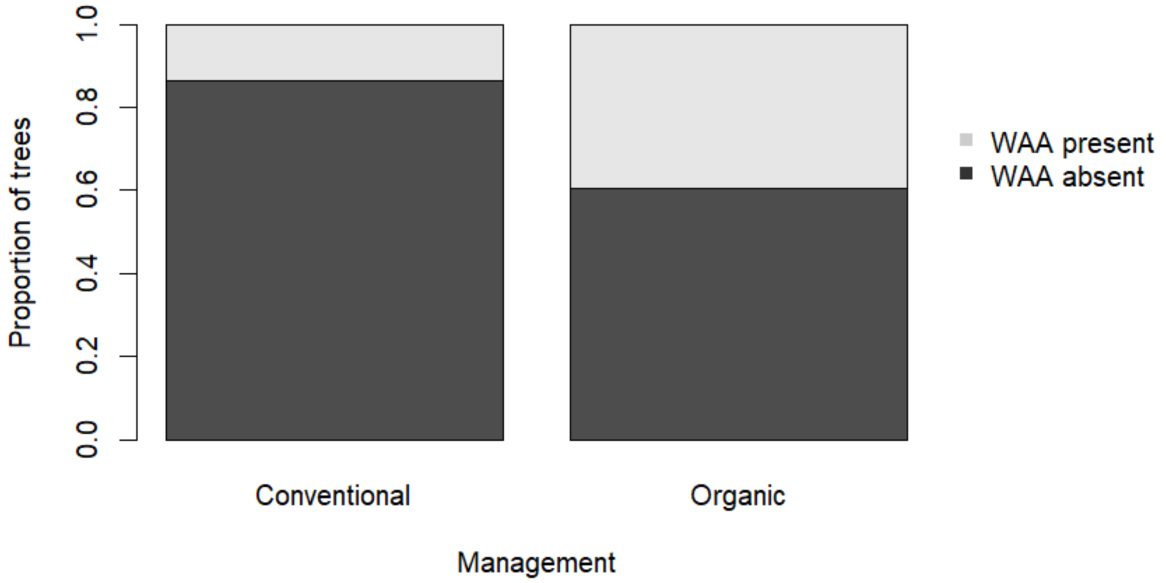

Figure 2.13. A bar chart showing the proportion of pseudo-trees which contained WAA which were managed conventionally (*n* = 100 trees, 300 pseudo-trees) or organically (*n* = 100 trees, 300 pseudo-trees). Data were collected in 2023.

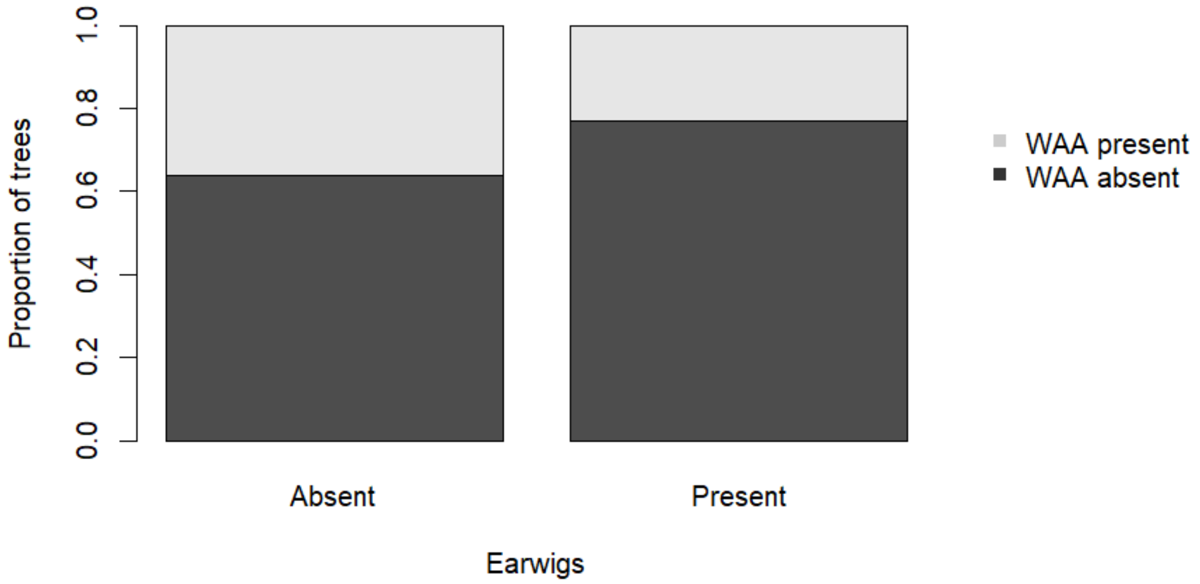

Figure 2.14. A bar chart showing the proportion of pseudo-trees which contained WAA where *F. auricularia* was absent (*n* = 172 pseudo-trees) or present (*n* = 428 pseudo-trees). Data were collected in 2023.

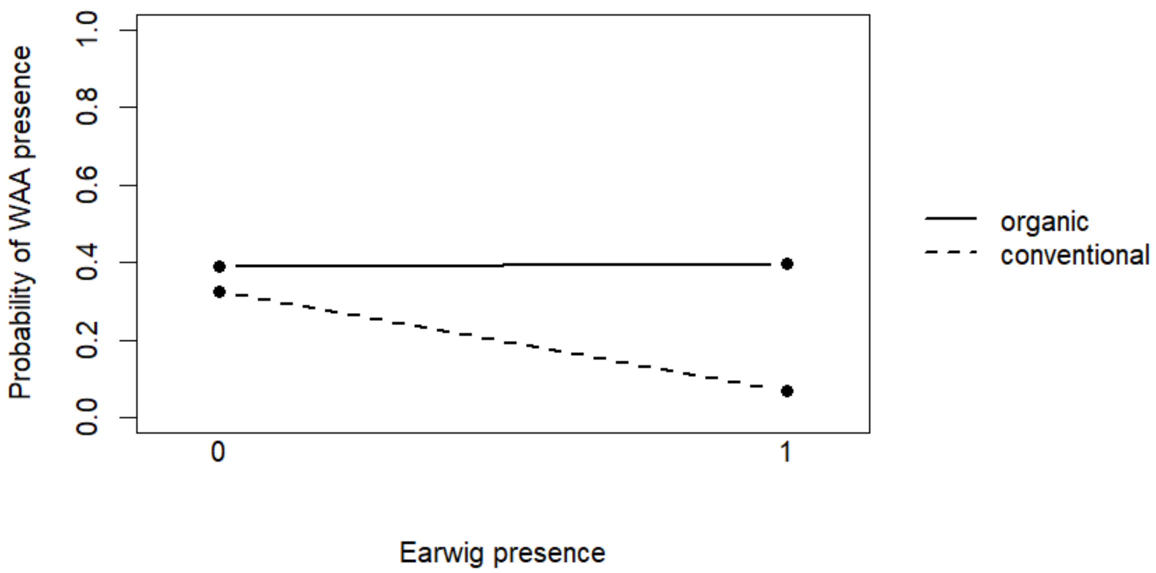

Figure 2.15. An interaction plot showing the effect of *F. auricularia* (earwig) presence (0 = Absent, 1 = Present) and management style on the probability of finding WAA in a tree. *n* conventional *F. auricularia* absent = 80 pseudo-trees. *n* conventional *F. auricularia* present = 220 pseudo-trees. *n* organic *F. auricularia* absent = 92 pseudo-trees. *n* organic *F. auricularia* present = 208 pseudo-trees. Data were collected in 2023.

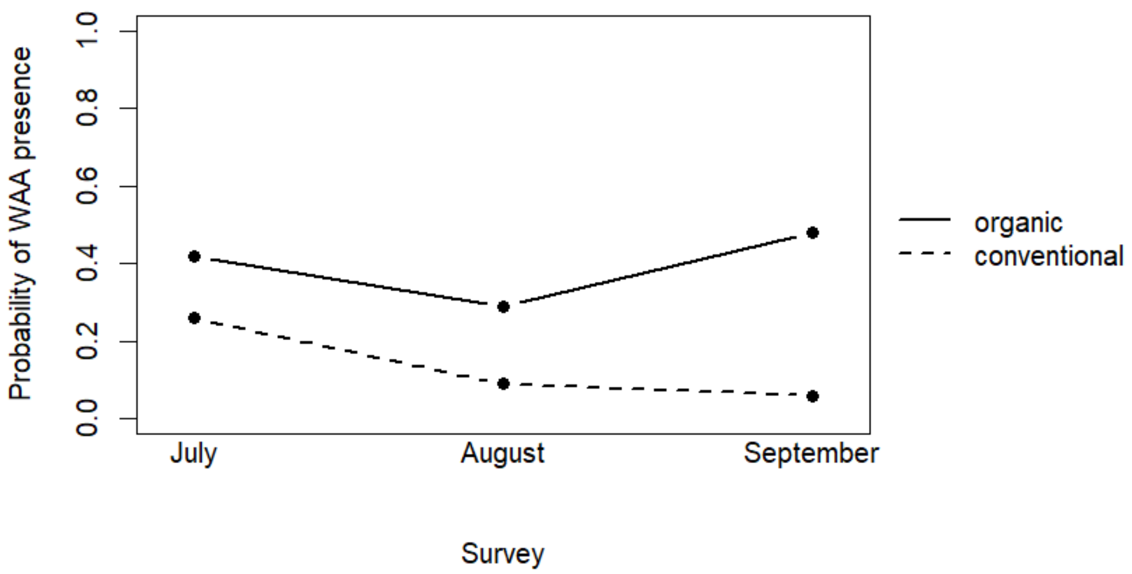

Figure 2.16. An interaction plot showing the effect of the month a survey was conducted and management style on the probability of finding WAA in a tree. *N* = 100 trees for all 6 datapoints. Data were collected in 2023.

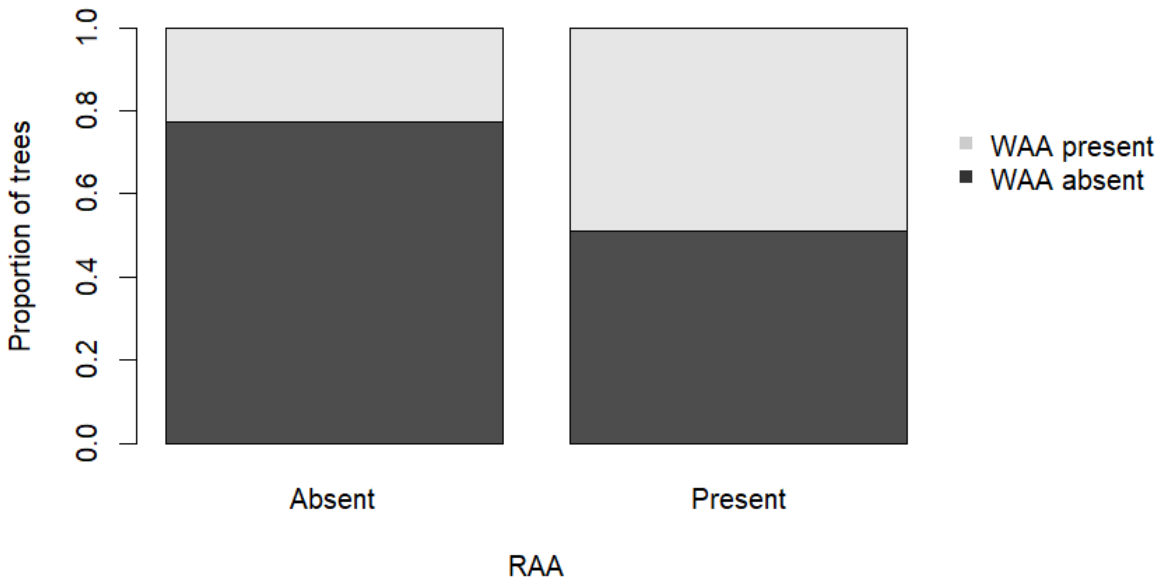

Figure 2.17. A bar chart showing the proportion of pseudo-trees which contained WAA where RAA was absent (*n* = 508 pseudo-trees) or present (*n* = 92 pseudo-trees). Data were collected in 2023.

The 2023 *F. auricularia* Baseline model (Table 2.13) 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 *F. auricularia* Assembled model (Table 2.14) 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 *F. auricularia* during the three months of surveys were observed (Figure 2.18), 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 *F. auricularia* when the row bed was > 50% bare earth (Figure 2.19). A tree was less likely to contain RAA if earwigs were present (Figure 2.20).

Table 2.13. 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 *F. auricularia* 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	*p* 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 2.14. 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 *F. auricularia* 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	*p* 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

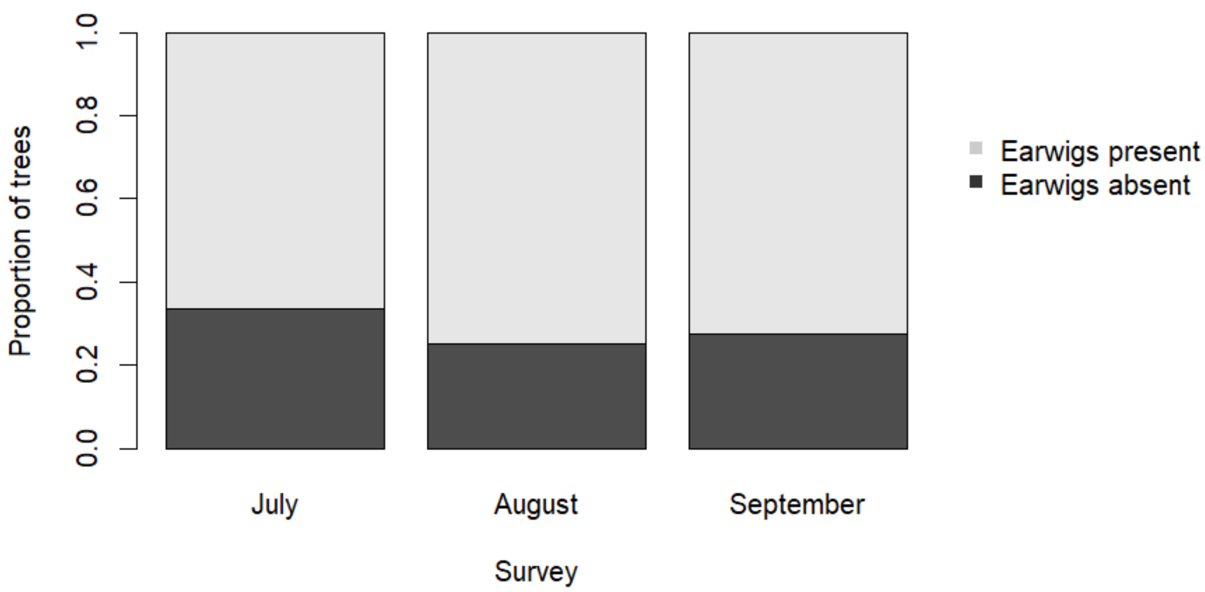

Figure 2.18. A bar chart showing the proportion of 200 trees containing *F. auricularia* during three surveys conducted in 2023.

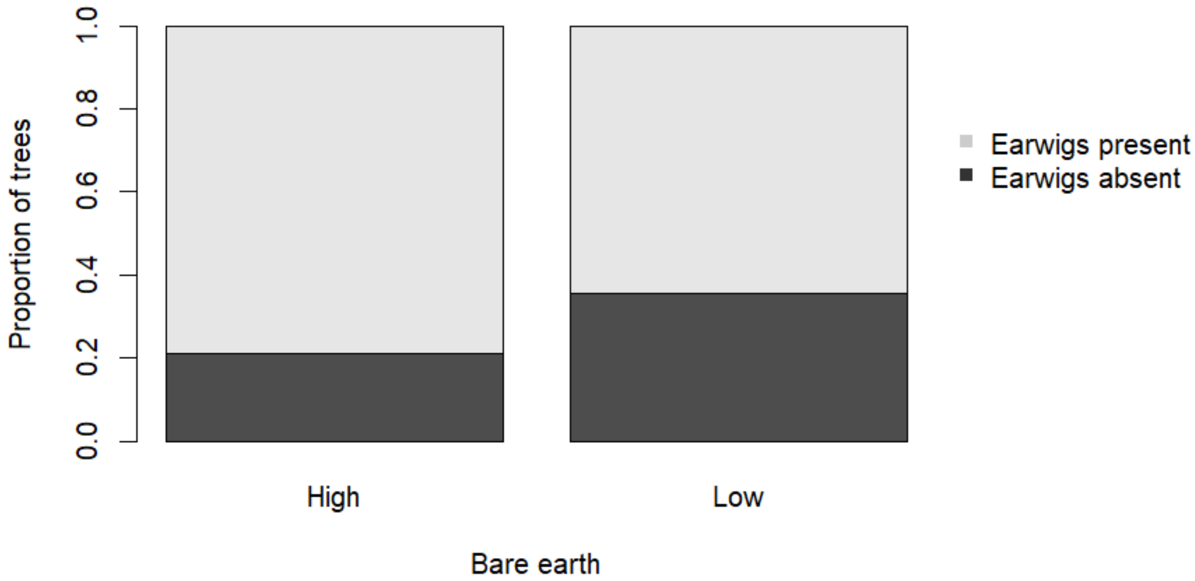

Figure 2.19. A bar chart showing the proportion of pseudo-trees which contained *F. auricularia* where the row bed was > 50% bare earth (High; *n* = 282 pseudo-trees, 94 trees) or < 50% bare earth (Low; *n* = 318 pseudo-trees, 106 trees). Data were collected in 2023.

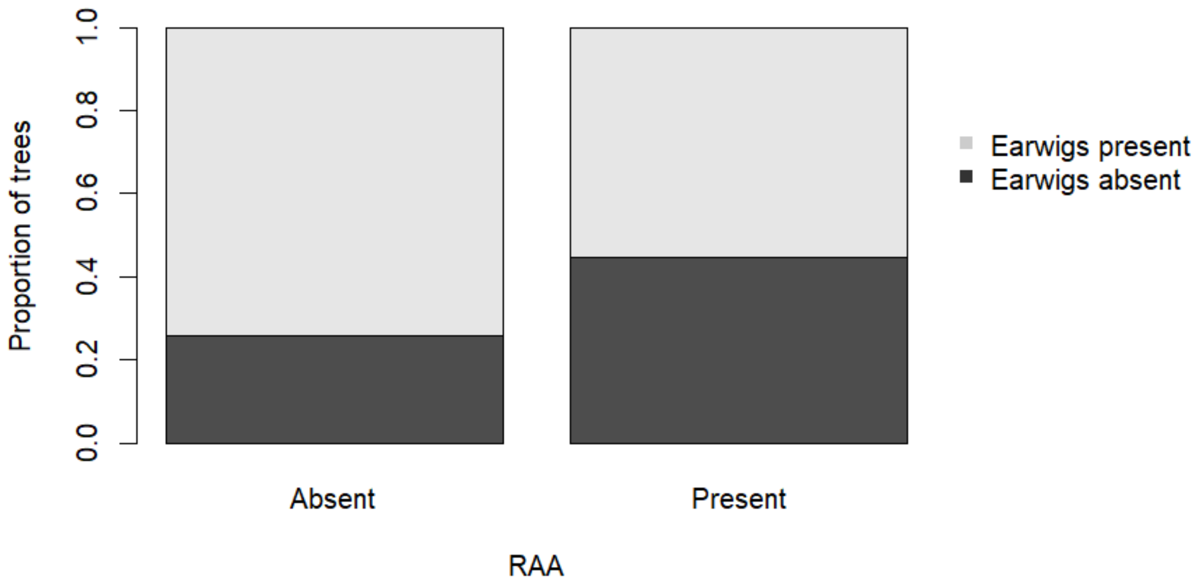

Figure 2.20. A bar chart showing the proportion of pseudo-trees which contained *F. auricularia* where RAA was absent (*n* = 508 pseudo-trees) or present (*n* = 92 pseudo-trees). Data were collected in 2023.

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 *F. auricularia* consumption of WAA.

Pitfall trapping detected *F. auricularia* in just two of the eight orchards. The pitfall traps in Orchard 12 contained a total of four *F. auricularia*, while the pitfall traps at Orchard 24 contained a total of 18 *F. auricularia*. These two orchards were the highest ranked in terms of the total *F. auricularia* count across all three 2023 surveys. Table 2.15 shows the pitfall trapping results.

Table 2.15. Summary information on the number of *F. auricularia* caught in five pitfall traps placed in different orchards (40 traps total). Days-standardised pitfall trap catch is the total pitfall trap catch for an orchard divided by the number of days traps were present. Total earwig count is the total number of *F. auricularia* caught in Wignest refuge traps from 30 pseudo-trees (n = 10 trees, 20 refuge traps) in the same orchard, earlier in the growing season. Data were collected in 2023.

Orchard	Management Style	Total Earwig Count	Pitfall Trap Catch	
			Total	Days-standardised
3	Conventional	6	0	0
9	Conventional	1477	0	0
10	Conventional	0	0	0
12	Conventional	1943	4	0.57
14	Organic	32	0	0
20	Organic	923	0	0
22	Organic	36	0	0
24	Organic	1513	18	1.80

2.4. Discussion

2.4.1. Management style and woolly apple aphid

In both years, organic *vs.* conventional management was a significant factor in the WAA Assembled model, with organic orchards containing a greater number of WAA-infested trees. Although there are numerous differences between organic and conventional management, it seems likely this was a direct result of synthetic insecticide sprays in conventionally managed orchards reducing the number of WAA. The available spray records showed that all but one of the conventional growers used spirotetramat (Batavia) sprays during the years of the surveys, with the other grower using flonicamid (Mainman®, Certis Belchim UK & Ireland, Cambridgeshire, UK). In contrast, the organic growers used FLiPPER® (Bayer Crop Science, Cambridge, UK), spinosad (Tracer®, Corteva Agriscience UK Ltd., Cambridgeshire, UK), and pyrethrins (Spruzit®, Certis Belchim). For the 2022 data, the comparison between organic and conventional management must be considered cautiously, due to the inclusion of only one organic grower in the surveys. However, the similar result obtained in 2023 with five organic growers in the survey suggests that organic management is more prone to WAA infestation. Happe *et al.* (2018) found more WAA in Spanish organic orchards than IPM orchards, but not in German orchards. Helsen *et al.* (2007) detected no difference in the abundance of WAA in organic and conventional orchards in Belgium and the Netherlands (no statistical analysis). In contrast to our study, Nicholas, Spooner-Hart and Vickers, 2005 found more WAA in orchard blocks sprayed with a broad-spectrum insecticide, compared with blocks that only used targeted disruption of non-WAA insects. There is therefore mixed evidence on how organic and conventional management affect the severity of WAA as a pest.

2.4.2. *Forficula auricularia* and woolly apple aphid

In both years, there was a negative correlation between *F. auricularia* presence and WAA presence. This is a promising result in terms of the biocontrol of WAA and suggests that unaugmented *F. auricularia* populations were providing beneficial control of WAA in the orchards studied. It is worth noting that in both years, only one of the two species' models showed this (the *F. auricularia* Assembled model in 2022, and the WAA Assembled model in 2023). The modelling process only statistically analyses correlation, so these results are not contrasting. The presence of WAA presence as a predictor for *F. auricularia* therefore does not imply that WAA is mechanically affecting the *F. auricularia* population. Instead, the most likely mechanism for this interaction in both models is *F. auricularia* predation of WAA making it less likely for both species to coexist in the same tree. The lack of all four models showing this effect suggests it is not the strongest factor impacting the presence of WAA. The most similar studies conducted so far, Happe *et al.* (2018) and Helsen *et al.* (2007), have differing results. The results of Helsen *et al.* (2007) are similar to this study, in that they found evidence indicating unaugmented *F. auricularia* populations were providing a measurable degree of control over WAA. In contrast, Happe *et al.* (2018) found no strong evidence for an influence of *F. auricularia* populations on WAA infestation. However, the results of this study also differ from both previous investigations in that the effect of *F. auricularia* on WAA was mediated by the management style of the orchards. In both years, the models which suggest *F. auricularia* presence is negatively correlated with WAA presence showed that this effect only occurred in the conventionally-managed orchards.

In organic orchards, the probability of a tree containing WAA remained almost identical regardless of the presence or absence of *F. auricularia*. While this result is, to the author's knowledge, novel, previous researchers have frequently discussed how the ecology of *F. auricularia* affects its role as a natural enemy of WAA (Gobin *et al.*, 2008a; Gontijo, Beers & Snyder, 2015; Quarrell, Corkrey & Allen, 2017; Orpet *et al.*, 2019a*). Forficula auricularia* has a year-long lifecycle, meaning the predation pressure it applies to WAA in each season will remain relatively constant. This contrasts with, for example, *A. mali*, which can reproduce rapidly in response to an abundance of WAA, leading to an increase within the season of *A. mali*-induced WAA mortality. *Forficula auricularia* is therefore most effective as a control agent for WAA when present early in the season, before WAA populations become well established (Quarrell, Corkrey & Allen, 2017; Orpet *et al.*, 2019a). Later in the season, WAA reproduction may accelerate, outstripping the rate at which *F. auricularia* can predate the aphids.

Gontijo, Beers & Snyder, (2015) highlight the synergy between generalist predators such as *F. auricularia* and *A. mali*. While the parasitoid wasp can slow the population growth of WAA, even at high WAA population levels, it cannot induce a decline in WAA abundance due to its reliance on WAA to reproduce (in ecological parlance, we would say the interaction between these species is bottom-up). *Forficula auricularia*, being highly polyphagous and omnivorous, is not reliant on WAA, and thus in the right circumstances is able to reduce or even eliminate WAA (top-down control). In this case, *F. auricularia* predation in conventional orchards may operate similarly to the synergy observed by Gontijo, Beers & Snyder, (2015), in that *F. auricularia* can control and eliminate WAA populations reduced by the application of spirotetramat or flonicamid.

In the organic orchards where WAA is more abundant, *F. auricularia* predation may not be sufficient to eliminate WAA from infested trees, hence the interaction effect detected in the models. It is important to note that *F. auricularia* will predate and therefore provide some control of WAA even in instances where WAA is not eliminated from a tree. *Forficula auricularia* may therefore still be of value in organic orchards. By modelling the presence and absence of these species, this analysis is conservative, and thus biased towards detecting an interaction effect with spray regime, because only complete elimination of WAA from a tree was considered by the current treatment of the survey data.

2.4.3. Survey month and woolly apple aphid

Woolly apple aphid aerial abundance can show a variety of patterns throughout a season; typically, abundance peaks in spring, crashes in the summer, and there is sometimes a second peak (often smaller) in the autumn (Brown & Schmitt, 1994; Heunis, 2001; Beers, Cockfield & Gontijo, 2010; Lordan *et al.*, 2015). As no survey was conducted in autumn of 2022, it is impossible to say if the number of occupied trees increased that year after the observed decline from July to September. In 2023, the month of the survey had an interaction with management style. There appeared to be a strong recovery of WAA populations in September of 2023 as compared with August, but only in organic orchards. In conventional orchards, the number of trees occupied by WAA continued to decline.

2.4.4. Moss and woolly apple aphid

The negative effect of moss presence in the row bed in 2023 on WAA presence was unexpected, and to the author’s knowledge no interaction between WAA and ground cover attributes has been previously recorded. It seems unlikely that mossy ground cover could directly influence aerial WAA colonies. Possibly there is an effect on edaphic (root-dwelling) WAA colonies. It may also be that mossy ground cover is merely correlated with an unmeasured factor, such as some facet of the microhabitat like temperature or moisture level. Given that this result was found only in 2023, it should be treated with caution, and warrants further investigation.

2.4.5. Rosy apple aphid and woolly apple aphid

The positive model parameter estimate for RAA presence on WAA presence seems likely to be a result of ecological similarities between these two species. Generalist predators will target both species, and because they both feed on the phloem of apple trees, aphidocidal systemic insecticides will impact both species simultaneously when applied.

2.4.6. Management style and *Forficula auricularia*

In the 2022 *F. auricularia* Assembled model, organic management appeared to have a negative impact on the number of trees occupied by *F. auricularia*. This result was not observed in the larger and better-structured 2023 dataset, suggesting that it may be an artefact of all of the organic orchards in 2022 belonging to a single grower. Happe *et al.* (2018) found no significant difference in the abundance of *F. auricularia* between organic and IPM orchards. They speculated that increased soil tillage in organic orchards may make them less suitable for overwintering *F. auricularia*, but that this effect might be compensated for by better prey availability. Helsen *et al.* (2007) found more *F. auricularia* in organic orchards than IPM orchards. Likewise, Simon *et al.* (2024) found conventional orchards had significantly lower *F. auricularia* abundance than organic or low-input orchards, but this changed when fewer broad-spectrum insecticides were used. Suchail *et al.* (2018) used biometry to investigate if the energy reserves and morphological traits of *F. auricularia* from organic orchards suggested they were under less stress (due to lack of insecticides) than *F. auricularia* from IPM orchards. They found *F. auricularia* caught in July from IPM orchards had lower body mass, lower energy reserves of both glycogen and lipids, and several morphological measures indicated they were smaller in size (all as compared with *F. auricularia* from organic orchards). However, the same research group completed a similar study on *F. auricularia* caught in October, and comparing conventionally managed orchards as well as IPM and organic (Le Navenant *et al.*, 2021). They found no significant differences in *F. auricularia* body mass, and idiosyncratic sex-specific differences in energy reserves between the management types. They did find that the average femur length for *F. auricularia* from conventional orchards was significantly shorter than those from organic and IPM orchards. The authors speculated that after the cessation of insecticide spraying in the growing season, *F. auricularia* in non-organic orchards are able to compensate for a lack of feeding earlier in the season to reach equivalent weights to *F. auricularia* in organic orchards, as a mechanism to explain the contrasting results of their studies. Jana *et al.* (2021) conducted a laboratory experiment where they exposed *F. auricularia* from organic or IPM orchards to chlorpyrifos-methyl contaminated food. Males showed higher mortality upon exposure than females, but for both sexes the *F. auricularia* collected from IPM-managed orchards showed significantly lower mortality than those from organic orchards. The lack of significant effect from management style on *F. auricularia* presence in this study is therefore partially supported by previous research.

2.4.7. Survey month and *Forficula auricularia*

The month of the survey had a significant effect on the number of trees occupied by *F. auricularia* in 2023. There appeared to be a small increase in the presence of *F. auricularia* from July to August, and then a small decline from August to September. Refuge trap catches in tree canopies tend to increase once *F. auricularia* nymphs begin to reach 5th instar (note the use of 5th instar as per Tourneur, Cole & Meunier, 2020), as they show a marked increase in their tendency to climb trees (Phillips, 1981; Dib, Sauphanor & Capowiez, 2017). Maturation of the population is thus the likely cause of the increase in the number of occupied trees from July to August. However, *F. auricularia* typically show a dramatic decrease in abundance when they mature from 5th instar to adulthood (Moerkens *et al.*, 2009), which was not detected in this study. It is possible that surveys in 2023 began late enough that the majority of *F. auricularia* had already moulted into adults, but if this were the case *F. auricularia* numbers would be expected to steadily decline during the study. It is also possible that any decline was compensated for by the fact that the Wignests were not replaced or moved during the experiment, as *F. auricularia* refuge traps tend to catch more individuals over time (Lamb, 1975; Phillips, 1981; Sauphanor & Sureau, 1993; Lordan *et al.*, 2015; Hanel *et al.*, 2023). It is also possible that in the surveyed orchards there was a high proportion of second broods, which can stabilise the population size (Moerkens *et al.*, 2009).

2.4.8. Ground cover and *Forficula auricularia*

Moss and algae were investigated in 2022 due to previous gut content analysis studies which have shown they are food sources for *F. auricularia* (Phillips, 1981; Orpet *et al.*, 2019a). While neither variable was included in the *F. auricularia* Assembled model for 2022, Moss score 1 (small patches of moss present in the row bed) did show as significant, with a positive effect on the likelihood of finding *F. auricularia*. Moss score was discarded as a variable in part because a trend was expected, *i.e.* if moss score 1 was positive, Moss score 2 would be expected to have a larger positive effect, which was not the case. In the 2023 *F. auricularia* Assembled model, moss presence was not significant, but the bare earth level (either < 50% ground cover or ≥ 50% ground cover) was significant, with more earwigs being present on trees when the row bed had a high bare earth cover. This effect is likely a result of *F. auricularia* nesting behaviour, as once leaving their nest *F. auricularia* tend to favour plant cover in the brief phase before they become mostly arboreal (Lamb, 1975). Burnip *et al.* (2002) also found a preference for bare ground by *F. auricularia*, when compared with pea straw mulch ground cover. However, they attributed this to the mulch competing with the refuge traps they used to measure *F. auricularia* abundance. There is evidence to suggest that *F. auricularia* eggs develop more quickly when the soil temperature is higher (Atwell, 1927; Lamb, 1974; Phillips, 1981), which may explain why *F. auricularia* was more frequently found in trees with high bare earth cover (Yu *et al.*, 2022). This result from 2023 may also explain why Moss score 2 (large patches of the row bed covered in moss) did not have a significant positive effect on *F. auricularia* presence in the 2022 model, as this score would be associated with low bare earth cover, unlike Moss score 1. None of the other ground cover measures were significant in the 2023 *F. auricularia* Assembled model. Plant cover and moss presence might both be expected to have some benefit to *F. auricularia* as food sources but, given the highly polyphagous nature of *F. auricularia*, it is perhaps unsurprising to find no significant correlation with any one food source.

2.4.9. Rosy apple aphid and *Forficula auricularia*

The negative effect of *F. auricularia* presence on the likelihood of a tree containing RAA is likely due to predation, as with WAA. While *F. auricularia* predation of RAA is less studied than WAA, there have been laboratory and field studies suggesting *F. auricularia* also provides RAA control (Dib *et al.*, 2016a, 2020).

2.4.10. Baseline and assembled *Forficula auricularia* comparison

When comparing the baseline to the assembled models, there is a particularly large discrepancy in the AIC of the 2023 *F. auricularia* models. This is likely due to the inclusion of orchard as a random effect in the Baseline model, while the Assembled model relies on measured fixed effects to explain the variation in *F. auricularia* presence. When looking at the untransformed *F. auricularia* counts for 2023 (Table A-3), large variations between orchards are present. Ultimately, the high AIC of the 2023 *F. auricularia* Assembled model relative to the Baseline model indicates that there were important differences between the various orchards that were not captured by the measurements taken in this study. Previous studies attempting to explain *F. auricularia* distribution within orchards have similarly struggled (Gobin *et al.*, 2007; Happe *et al.*, 2018).

2.4.11. Pitfall trapping

While the pitfall trapping carried out as part of this study was not comprehensive, it was sufficient to show that the pitfall trap catch of *F. auricularia* appeared to be positively correlated with tree refuge trap catch; *F. auricularia* were only caught in pitfall traps in the two orchards with the highest total refuge trap catches. This indicates that where refuge trap catches were low, it is unlikely that a large population of *F. auricularia* was present undetected on the ground. There was also no stark difference in the number of *F. auricularia* caught in pitfall traps between organic and conventionally managed orchards.

2.4.12. Orchard age

Orchard age was discarded as a factor from modelling. Exploration of the data revealed no clear pattern for either WAA or *F. auricularia* presence with age. The idea that older and larger trees contain more shelter for both WAA and *F. auricularia* is sometimes mentioned by researchers (Theobald, 1920; Phillips, 1981; Beers, Cockfield & Gontijo, 2010), but there is a lack of empirical evidence for such an effect in either species. Recently, Bischoff *et al.* (2024) showed that both environmental complexity and the population density of *F. auricularia* mediate the ability of *F. auricularia* to effectively control WAA populations. If it is true that older trees contain more shelter for both species, then this may result in a net-neutral effect in terms of *F. auricularia* control of WAA.

2.4.13. Molecular gut content analysis

In both years of the study, the molecular gut content analysis showed low levels (5% of *F. auricularia* sampled) of detectable predation when compared with previous studies (Romeu-Dalmau, Piñol & Agustí, 2012; Orpet *et al.*, 2019a). Many improvements were made to the molecular gut content analysis methodology between the two years. In particular, attention was given to the half-life of detectability, and the fact that in the field any *F. auricularia* consumption of WAA is likely to occur at night. A preliminary study estimated that the half-life of detectability for an *F. auricularia* consuming a single WAA, and then processed using this methodology, was approximately 10 hours (Tempest, unpublished data), which is in line with other published results (Greenstone *et al.*, 2007). Romeu-Dalmau, Piñol & Agustí, (2012) estimated a half-life of detectability for *F. auricularia* consumption of *Aphis spiraecola* (Patch) of 23.8 hours, but their methods had numerous differences from those used in this study. Multiple aphids were fed to each *F. auricularia*, the same DNA extraction kit was used but without any modification of the protocol, and a different aphid species, primers, dissection method, and PCR method were used, all of which may influence the half-life of detectability. If the estimated half-life of 10 hours is assumed to be accurate, then even in 2023 when molecular collections were carried out early in the morning, a substantial proportion of potentially positive results might have decayed by the time *F. auricularia* were put on ice.

Despite the improvements made from 2022 to 2023, there was not a large increase in the proportion of positive results. It is possible that some other stage of the methodology is inadequate. In particular, the tissue homogenisation and lysis may not have been thorough, and the author would recommend investigating adaptations to the method used here. It is also possible that the level of WAA (and other aphid species) consumption was simply much lower than that found in other studies (Romeu-Dalmau, Piñol & Agustí, 2012; Orpet *et al.*, 2019a), which were conducted in other countries and potentially with very different agricultural systems.

The results of the molecular gut content analysis are also rendered less informative by the lack of primer specificity that was discovered. Without further sequencing of the samples, it is impossible to say how many of the ‘positive’ results are in fact *R. padi* rather than WAA. There is also the possibility that other untested aphid species’ DNA may be amplified by the primers used. The primers were initially designed and tested within the context of the apple orchards in Washington state, USA, and it may be the case they are less suitable for use outside of that context. Assuming that some portion of the ‘positive’ results are in fact WAA DNA, then this study may provide evidence for *F. auricularia* consumption of WAA occurring in both organic and conventional orchards, and at levels of WAA infestation where colonies were not visible upon visual inspection of the tree.

2.4.14. Soil firmness and *Forficula auricularia*

The soil firmness profiles showed that at depths closer to the surface, all of the orchards were similar. *Forficula auricularia* nesting depths are typically from 2 to 10 cm (Lamb, 1974), and the soil firmness of the orchards in 2022 was most similar at depths closer to the surface. Soil drainage is sometimes speculated to affect *F. auricularia* populations (Crumb, Bonn & Eide, 1941; Phillips, 1981), and soil temperature and tillage both have strong effects on *F. auricularia* development and mortality (Atwell, 1927; Lamb, 1974; Moerkens *et al.*, 2012). However, soil firmness did not show any clear pattern with *F. auricularia* abundance in the 2022 surveys. Lamb (1974) suggested that *F. auricularia* nest excavation and structure may be adaptable depending on “peculiarities of soil and location”. It may be that such adaptations to their nest-building behaviour allow *F. auricularia* to compensate for differences in soil firmness such that it does not affect their abundance.

2.5. Conclusions

Overall, the results of the surveys carried out are positive for the potential biocontrol of WAA. There is good evidence that *F. auricularia* is providing useful control of WAA at naturally occurring abundances, without the need for augmentation. However, *F. auricularia* may not be able to eliminate WAA from trees entirely without ‘assistance’ from chemical insecticides. The distribution of *F. auricularia* remains frustratingly difficult to explain, with high variation between orchards which is not fully explained by the measurements taken in this study. Characteristics such as soil temperature, soil infiltration and ground cover should be investigated further. Aspects of the molecular gut content analysis approach taken here may be useful for other researchers, but the method should not be adopted wholesale.

3. Impact of artificial shelters on the numbers of *Forficula auricularia* and *Eriosoma lanigerum* in an experimental apple orchard

3.1. Introduction

The common European earwig, *Forficula auricularia* (L.), is a highly polyphagous omnivorous insect that occurs in a wide variety of environments (Beall, 1932; Lamb, 1975; Lamb & Wellington, 1975). As the common name implies, *F. auricularia* is native to Europe, as well as western Asia, but has been introduced by human activity to North America, Australia, New Zealand, and parts of South America (González Miguéns *et al.*, 2020; Maczey, 2022; Pavón-Gozalo *et al.*, 2011; Quarrell *et al.*, 2018). Across this range, *F. auricularia* can be found occupying households, gardens, woodlands, and agricultural crops ranging from grains (Binns *et al.*, 2021) to strawberry (*Fragaria x ananassa*, Duchesne; Englert & Herz, 2019) and to apple (*Malus domestica,* Borkh; Helsen *et al.*, 2007; Phillips, 1981). While *F. auricularia* can directly damage softer and thinner-skinned fruits, in other crops, including apple, *F. auricularia* is less capable of primary damage, and instead is often considered a beneficial organism due to the predation of more serious invertebrate pests (Evans & Longépé, 1996; Orpet, Crowder & Jones, 2019b).

Woolly apple aphids (WAA), *Eriosoma lanigerum* (Hausmann), feed on the woody tissue of apple trees both above (scion) and below ground (root stock; Marcovitch, 1934). When feeding, WAA release saliva containing toxins that cause swelling and deformation of the plant tissue (known as galling; Wool, 2004). This damages apple trees by interfering with the transportation of nutrients (Brown *et al.*, 1995). In addition, severe galling can open wounds in the bark, which act as sites where pathogens may gain entry to infect the internal tissue of the tree, in particular apple canker (*Neonectria ditissima*, Samuals and Rossman; 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 (Guerrieri & Digilio, 2008).

The authors of several exclusion studies designed to prevent crawling insect pests from climbing the trunks of apple trees have demonstrated that this practice also inhibits *F. auricularia* from reaching the tree canopy. As a result of excluding *F. auricularia* from the tree canopies in this way, WAA infestations became more severe (Gontijo, Beers & Snyder, 2015; Mueller, Blommers & Mols, 1988; Nicholas, Spooner-Hart & Vickers, 2005; Orpet *et al.*, 2019b). This has led to *F. auricularia* being considered an important natural enemy of WAA.

Besides exclusion studies, the other main type of evidence suggesting *F. auricularia* are important predators of WAA is correlational, namely that high earwig populations in apple orchards are associated with low numbers of WAA (Alins *et al.*, 2023; Hanel *et al.*, 2023; Helsen *et al.*, 2007; Mueller, Blommers & Mols, 1988; Nicholas, Spooner-Hart & Vickers, 2005; Orpet *et al.*, 2019a; Quarrell, Corkrey & Allen, 2017; Stap *et al.*, 1987). However, these population studies have almost exclusively relied on refuge trapping as a method of monitoring earwig numbers. While refuge trapping is an effective method of monitoring *F. auricularia*, there are various factors which can affect the occupation of refuge traps, and the method necessarily involves altering the environment, discussed further below.

Many trapping methods use an attractant, *e.g.* gustatory (food), olfactory (semiochemicals) or visual (*e.g.* colour, pattern, *etc.*), or rely on animals entering traps by chance, after which the trap will prevent the animal from escaping. A typical refuge 'trap' is different in that it offers insects an attractive shelter but does not typically employ a mechanism of preventing insects from escaping. Researchers can study the population by monitoring the occupation of the shelter. While it may seem counterintuitive to refer to a structure which the insect is freely capable of escaping from as a ‘trap’, a ‘refuge trap’ or ‘refuge trapping’ is the common terminology used to describe artificial shelters which have been provided with the intent of either monitoring a population, or collecting study organisms. A particularly well-researched application for refuge trapping is in the study of crayfish (Decapoda: Astacidea; Curti, Fergus & Palma-Dow, 2021; Green *et al.*, 2018; Walter, 2012). Because animals can freely enter and leave a refuge trap, the trap will catch a larger proportion of the local population of the target organism if it is comparatively more attractive (or more abundant) than the natural shelters available, and is therefore more likely to be selected as a shelter by insects.

In this chapter, a ‘refuge trap’ will be considered a specific instance of an ‘artificial shelter’, which has been deployed by researchers with the purpose of monitoring a population of *F. auricularia*. Where an artificial structure has been provided for a different purpose, it will be referred to only as an ‘artificial shelter’ and not as a refuge trap. This distinction can be helpful when trying to understand previous *F. auricularia* research. For example, Lamb (1975) used different deployments of the same device as both a means of experimentally altering the environment (artificial shelter), and as a way to monitor any change in the *F. auricularia* population (refuge trap).

Shelters are used by *F. auricularia* during the day; natural shelters in apple trees typically consist of crevices in bark, dense clusters of fruit, and tightly rolled leaves or leaf clusters, although any space which fulfils the positive thigmotaxis of *F. auricularia* will induce them to shelter (Phillips, 1981). Artificial shelters usually consist of multiple narrow tubes, grooves, or channels in close proximity; examples include tightly rolled corrugated cardboard, bundles of young bamboo canes, or wooden boards with channels carved into them (Figure 3.1). These provide tight spaces, darkness, and protection from rain and desiccation. Importantly, they also provide shelter in greater volume than a typical natural shelter provides. This makes them effective for monitoring *F. auricularia* due to their preference for aggregating while sheltering during the day; all other things being equal, *F. auricularia* will preferentially occupy one large artificial shelter rather than several smaller natural ones (Lamb, 1975). The chemical ecology of *F. auricularia* aggregation is complicated, with different studies finding attraction or repulsion to cuticular washes from *F. auricularia* conspecifics depending on the sex and life stage of both the donor and the responder (Hehar, Gries & Gries, 2008; Hehar, 2007; Quarrell *et al.*, 2016; Walker, Jones & Fell, 1993). Quarrell *et al.* (2016) suggested these contradictory results may be the due to changes in *F. auricularia*’s response to pheromones throughout their life cycle. However, the preference of *F. auricularia* for artificial shelters occupied (or previously occupied) by conspecifics has been demonstrated by several studies, and is believed to be one reason these shelters tend to become more effective over time (Hanel *et al.*, 2023; Lamb, 1975; Lordan *et al.*, 2014; Phillips, 1981; Sauphanor & Sureau, 1993).

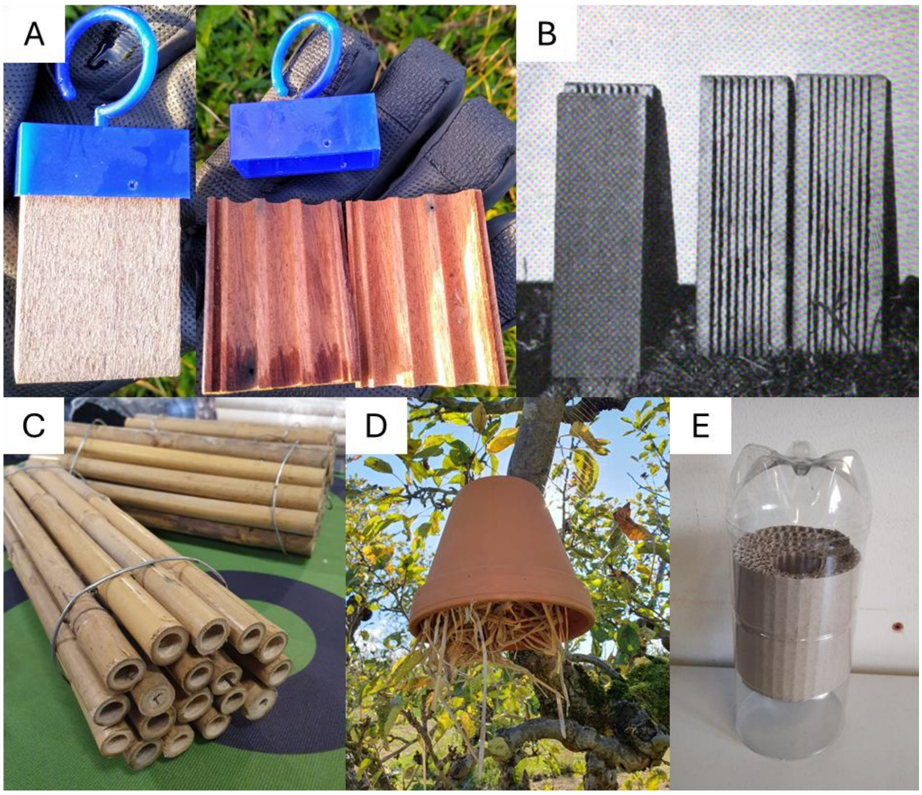

Figure 3.1. Examples of artificial shelters used to provide shelter for earwigs (*Forficula auricularia*). A) A prototype Wignest™ (Russel IPM Ltd, Flintshire, United Kingdom). B) A shelter made from wooden groove boards, taken from Crumb, Bonn & Eide (1941). The boards on the left show the typical deployment, while the two sets of boards on the right are reversed to show the grooves. C) A shelter made from a bundle of bamboo canes. These are typically deployed horizontally (as pictured) to prevent rain entering the canes. D) A shelter made from an upturned flowerpot filled with straw, deployed at the Royal Horticultural Society Garden, Wisley. E) A shelter made from corrugated cardboard, with a plastic bottle as waterproofing.

There are few studies which have monitored *F. auricularia* in the field without the use of refuge trapping. Video monitoring of WAA colonies observed *F. auricularia* feeding on them with a higher frequency than any other generalist predator species (coccinellids, chrysopids, and syrphids; Orpet, Crowder & Jones, 2019a). Lamb (1975) attempted to use fluorescent paint to observe *F. auricularia* foraging, but individuals were difficult to find subsequently and were also observed to cease moving when illuminated by the UV lamp.

Logan *et al.* (2007) is perhaps the best example of a study comparing *F. auricularia* populations with artificial shelters to a population without additional shelters. The number of *F. auricularia* occupying kiwifruit (*Actinidia chinensis*; Planch) vines with artificial shelters was compared to vines without artificial shelters. This was performed by removing and destructively searching pruning stubs and dead leaves, as well as searching and emptying the artificial shelters themselves after a 36-day trial period. The two treatments were also compared by assessing the amount of *F. auricularia* frass left in clear plastic tubes at the top of each kiwifruit vine, which had been filled with an artificial insect diet. They found no significant difference in the total population of *F. auricularia* occupying vines that had artificial shelters added from unaltered vines, and, on the vines with artificial shelters added, there was no correlation between the number of *F. auricularia* in the artificial shelter and the number of *F. auricularia* utilising natural shelters. There was also no significant difference in the proportion of feeding tubes with *F. auricularia* frass on them between the two treatments. The authors also marked and monitored diapsid scale insects in both treatments and found no significant difference in the level of scale-insect predation between the vines which had artificial shelters and control vines. They concluded that natural shelters were abundant enough not to be a limiting factor in kiwifruit vines, but other research has suggested this may not be the case for apple trees (Moerkens *et al.*, 2009; Jana *et al.*, 2021).

Lamb (1975) conducted an experiment where two 5 m^2 plots of dense vegetation with artificial shelters added to them were compared with two similar plots without shelters added. These shelters consisted of wooden boards with grooves carved into them, which were then placed on the ground in a regularly spaced pattern. The same type of device was also used as a refuge trap in this experiment. Each week, for a month, the artificial shelters were emptied and removed, and then refuge traps were added to all four plots for one night before being emptied and removed. In the 'shelter added' plots, the artificial shelters were then replaced. The total number of *F. auricularia* in each plot was calculated and at the end of the experiment the artificial shelters were removed from the 'shelter added' plots but not emptied. Refuge traps were then deployed as before. This experiment found that the 'shelter added' plots had significantly higher numbers of *F. auricularia* than the control plots during the experiment. At the end of the experiment, when the *F. auricularia* using the artificial shelters had been removed before adding the refuge traps, the final trap catches from the 'shelter added' plots were not significantly lower than the control plots. Given that any *F. auricularia* occupying the artificial shelters had been removed from this final population count, this suggests that adding artificial shelters increased the population size of *F. auricularia* living in those plots. The author posited this may have been due to a decreased level of predation by birds.

To the author's knowledge, Jana *et al.* (2021) is the only study conducted in apple orchards which compared blocks with artificial shelters to blocks without them. They compared two types of artificial shelter: one wrapped directly around the trunk, and one rolled tightly about itself and then attached to the trunk. Orchard blocks containing the tightly rolled shelters were found to contain significantly more *F. auricularia* than control blocks or those with the other type of shelter when the tree canopies were tap sampled during the daytime. They did not investigate if this increased the suppression of any pest species.

Earwigs have one generation per year, and hence population size cannot increase substantially within a single growing season by adding artificial shelters. However, the addition of artificial shelters to certain trees in an orchard could potentially serve to concentrate the *F. auricularia* population onto individual trees, or work to reduce the within-season mortality rate (Lamb, 1975) by providing shelter not available elsewhere in the orchard. Provided artificial shelters are introduced and maintained for several years, the *F. auricularia* population could increase over time, if availability of shelters was a limiting factor (Berryman & Hawkins, 2006).

Shelter availability is a population-limiting factor across a wide range of taxa, from wolves (*Canis lupus*) to other invertebrates such as mantis shrimp (Stomatopoda) and spongy moth (*Lymantria dispar*, L.; Campbell, Hubbard & Sloan 1975; Steger, 1987; Grilo *et al.*, 2019). *Forficula auricularia* population dynamics are poorly understood, and it is not clear if shelter is often a limiting factor in apple orchards. Moerkens *et al.* (2009) studied density dependency in *F. auricularia* populations, comparing apple and pear orchards. While they could not look at the number of individuals using long-term natural shelters such as bark, when fruit clusters were removed in harvest, the number of *F. auricularia* in refuge traps increased in pear orchards but not in apple orchards, suggesting apple fruit clusters do not provide as much shelter as pear fruit clusters. Besides the work of Jana *et al.* (2021), this is the best evidence of shelter availability as a population-limiting factor for *F. auricularia* in apple orchards. It is important to note that this may not be the case for all apple varieties, colloquially short-strig varieties are suggested to shelter more *F. auricularia* in them due to the denser clusters.

Fountain (2018) reviewed the insecticides used in apple and pear orchards which can harm *F. auricularia*. The synthetic insecticides spinosad, indoxacarb and chlorpyrifos-methyl can have sublethal effects and kill *F. auricularia* in apple orchards, while sublethal exposure to deltamethrin can significantly impair maternal care (Jana *et al.*, 2021; Meunier *et al.*, 2020). Happe *et al.* (2018) and Nicholas, Spooner-Hart and Vickers (2005) showed that targeted insecticide use in IPM (Integrated Pest Management) strategies did not negatively impact *F. auricularia* abundance, and organic orchards did not have significantly more *F. auricularia*.

In the past, WAA was often controlled coincidentally through the use of broad-spectrum insecticides, particularly organophosphates, applied for other pests of apple (Beers, Cockfield & Fazio, 2007). With the advent of more targeted synthetic or biological control measures, WAA has been released from the incidental control provided by organophosphate insecticides, and this is speculated to be one of the major reasons for the increasing frequency of WAA infestations in apple orchards (Bangels *et al.*, 2021; Beers, Cockfield & Fazio, 2007; Beliën *et al.*, 2010). Modern chemical control typically relies on systemic pesticides due to their ability to circumvent the protection provided by both the eponymous 'wool' of WAA, and their ability to survive underground on the rootstock. In the United Kingdom (UK), the Apple Best Practice Guide (Cross *et al.*, n.d.) states that Mainman (Certis Belchim, Cambridgeshire, UK), containing the active ingredient flonicamid, is effective for WAA control. In recent years, however, growers have reported flonicamid and other approved insecticides as having reduced effectiveness in controlling WAA. The guide also recommends Batavia (Bayer Crop Science, Cambridge, UK), containing the active ingredient spirotetramat, as the only remaining effective option. Spirotetramat is a two-way systemic keto-enol insecticide, meaning it is transported by both the xylem and phloem of the plant and can therefore reach WAA feeding on the roots, and inhibits lipid biosynthesis (Nauen *et al.*, 2007; Schoevaerts *et al.*, 2011). Spirotetramat was, by area treated, the third most-used insecticide on apple in the UK in 2022 (Ridley *et al.*, 2024) and has an extension of use in Great Britain for use against WAA specifically (EAMU Number 1261, 2022).

The objective of this study was to determine whether historical insecticide use, and the availability of artificial earwig shelters, changed *F. auricularia* population densities and WAA presence in orchard blocks.

3.2. Methods

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 3.1 gives the names, active ingredients, and frequencies of the insecticide sprays applied to the Royal Gala trees (see Table A-6 for the available details of each spray).

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 3.1. 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.

		Number of Sprays per Block				IOBC Toxicity Rating	
Active Ingredient	**Block**	**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. 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 the majority of colonies occurring on the branches.

3.2.3. *Forficula auricularia* assessment

Forficula auricularia 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. *Forficula auricularia* were categorised as male, female, or immature (no immature *F. auricularia* were recorded), based on the shape of the cerci. Adult male *F. auricularia* have strongly curved cerci, while female cerci are much straighter with only a slight curve at the tip. Immature *F. auricularia* 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 *F. auricularia* searches were completed after sunset (earliest search started at 22:15, latest search started at 02:20).

3.2.4. Statistics

As the *F. auricularia* 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 *F. auricularia* counts between the different orchard blocks, excluding Block 7 which contained the artificial shelters.

The impact of artificial shelters (used by *F. auricularia*) 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), lmtest (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 3.2). 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 3.2. 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. Results

3.3.1. *Forficula auricularia* assessment

There was no significant difference in the number of *F. auricularia* 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 3.2).

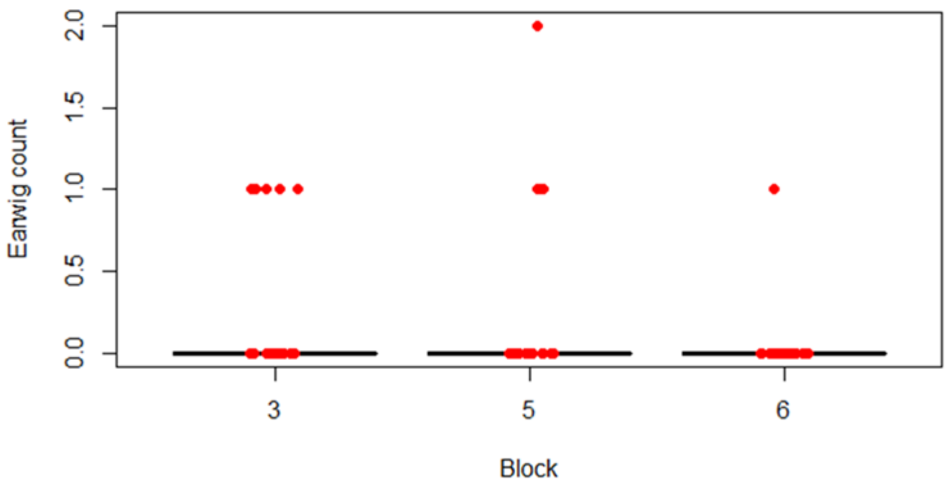

Figure 3.2. Boxplot of earwig (*Forficula auricularia*) counts from Royal Gala apple (*Malus domestica*) trees in different orchard blocks which did not contain artificial *F. auricularia* shelters (*n* = 22 in all cases). Datapoints are superimposed in red.

When the effect of artificial shelters was tested, significantly more *F. auricularia* were recorded on apple trees with shelters (Wilcoxon test: *n* without shelter = 22, *n* with shelter = 22, W = 59, *p* < 0.001; Figure 3.3). This test was completed by comparing Block 6 to Block

7, due to the similarity in their history of insecticide treatment (Table 3.2). 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.

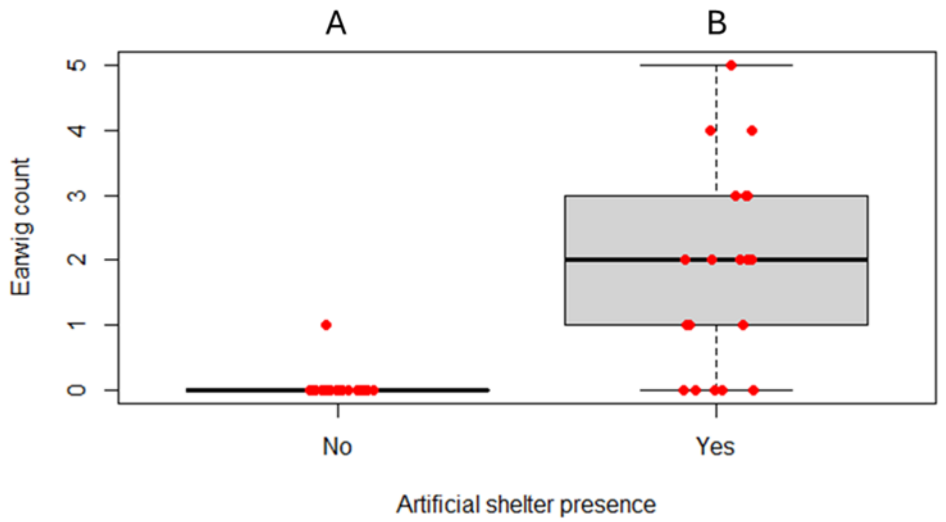

Figure 3.3. Boxplot of earwig (*Forficula auricularia*) counts from Royal Gala apple (*Malus domestica*) trees in orchard blocks which either did (n = 22) or did not (n = 22) have artificial shelters for *F. auricularia*. Data come from blocks with similar histories of insecticide use. The datapoints are superimposed in red. Groups which do not share a letter are significantly different ($p < 0.05$).

Artificial shelters were associated with significantly higher numbers of *F. auricularia* in apple trees at night (Wilcoxon test: n without shelters = 66, n with shelters = 22, W = 214.5, $p < 0.001$; Figure 3.4).

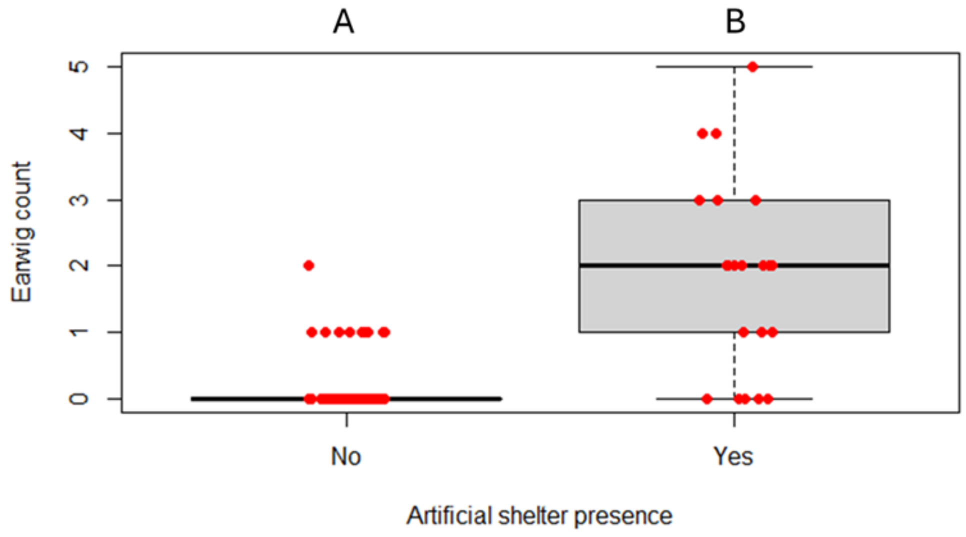

Figure 3.4. Boxplot of earwig (*Forficula auricularia)* counts from Royal Gala apple (*Malus domestica*) trees in orchard blocks which either did (n = 22) or did not (n = 66) have artificial shelters for *F. auricularia*. These data come from orchard blocks with various histories of insecticide use. Datapoints are superimposed in red. Groups which do not share a letter are significantly different ($p < 0.05$).

3.3.2. 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 3.5). These blocks were selected for comparison due to their similar histories of insecticide treatment (Table 3.2).

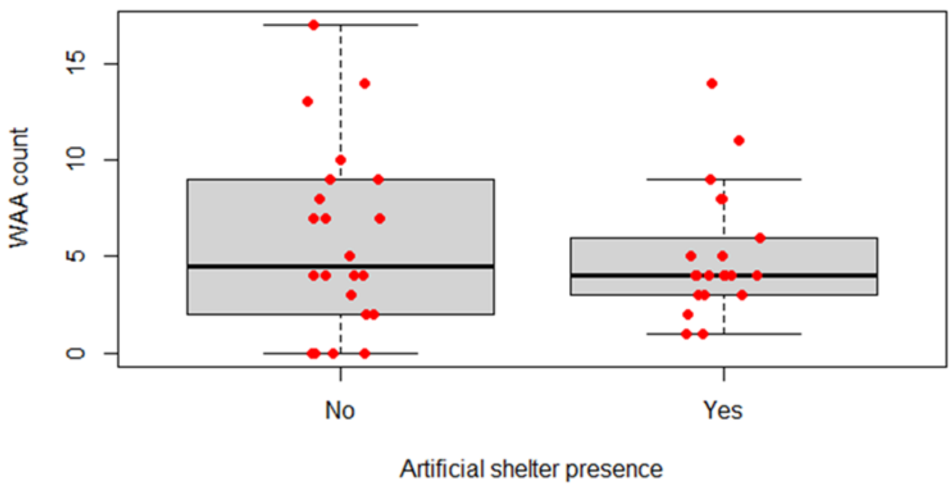

Figure 3.5. Boxplot of woolly apple aphid (*Eriosoma lanigerum*) colony counts from Royal Gala apple (*Malus domestica*) trees in orchard blocks which either did (n = 22) or did not (n = 22) have artificial shelters for *Forficula auricularia*. These data come from blocks with similar histories of insecticide 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 3.6). 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.

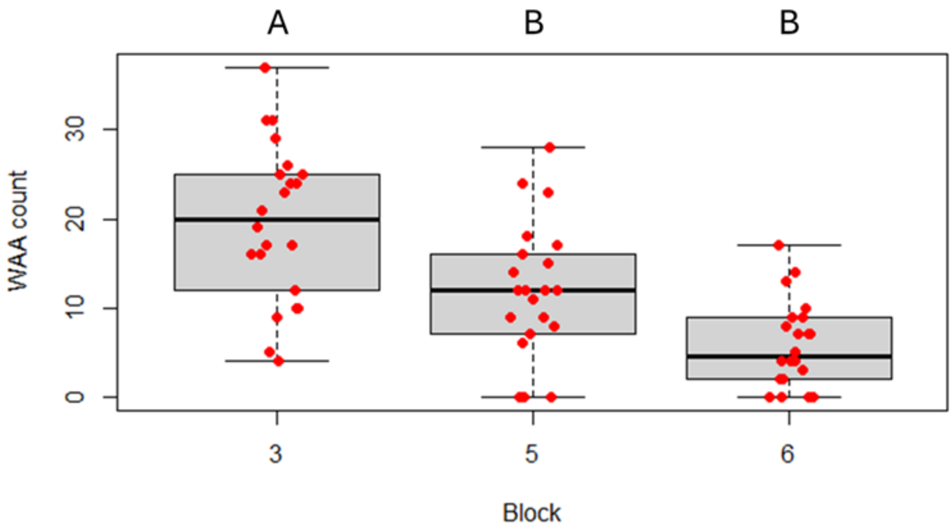

Figure 3.6. Boxplot of woolly apple aphid (*Eriosoma lanigerum*) colony counts from Royal Gala apple (*Malus domestica*) trees in orchard blocks with different histories of insecticide use. These data include only blocks without artificial shelters. The datapoints are superimposed in red. Groups which 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 3.5), 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 3.7). 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 ($p = 1.00$).

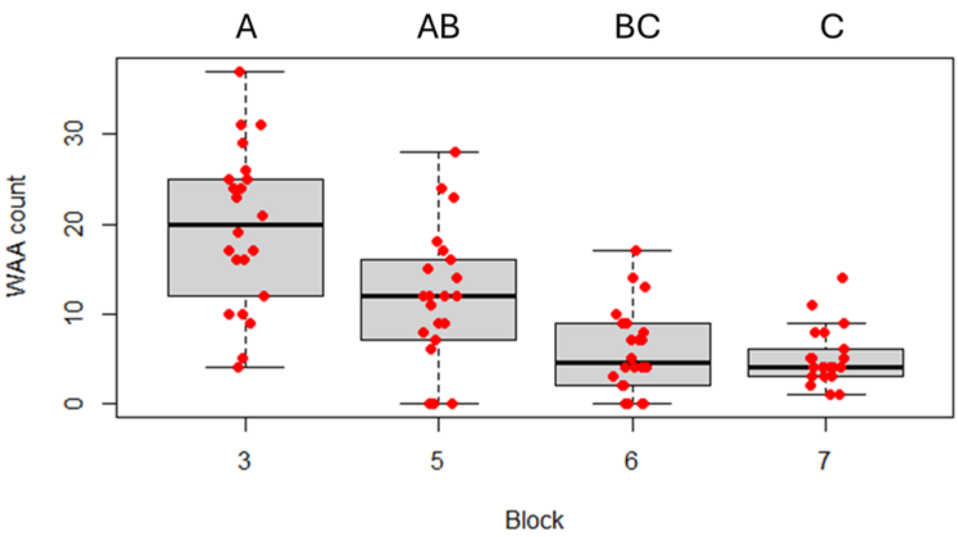

Figure 3.7. Boxplot of woolly apple aphid (*Eriosoma lanigerum*) colony counts from Royal Gala apple (*Malus domestica*) trees in orchard blocks with different histories of insecticide use. These data include a mix of blocks with and without artificial shelters. The datapoints are superimposed in red. 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 3.2) and hence WAA colony count per tree did not seem to be related to past insecticide applications.

3.4. Discussion

Two key findings from this study are that: 1) the presence of corrugated cardboard shelters around the tree trunks led to significantly higher numbers of *F. auricularia* active in the canopy of apple trees at night, and 2) the number of WAA colonies was significantly different between the orchard blocks but was not affected by the presence of earwig shelters. However, it is important to note that the design of this experiment when considering earwig shelter *vs.* no earwig shelter was not fully replicated and randomised, weakening the conclusions that can be drawn from the data. This was due in part to established studies being run concurrently in the same experimental orchard.

Generally, these results suggest that the corrugated cardboard bands applied to Block 7 acted as artificial shelters for *F. auricularia*, and resulted in an increased number of *F. auricularia* found on these trees at night. Conversely, the presence of artificial shelters and increase in *F. auricularia* did not lead to a significant reduction in the number of WAA colonies. Hence, it is not clear from this replicate-limited study whether there was an interaction between *F. auricularia* and WAA.

However, there was a significant difference between the numbers of WAA colonies in the different orchard blocks; historical differences in spray regime were initially pursued as an explanation. Previous studies have shown broad-spectrum insecticides can lower the rate of reproduction for multiple generations after exposure, for example in the spider *Alpaida veniliae* (Keyserling), *Diaeretiella rapae* (M'Intosh) a species of wasp, or the ant *Lasius niger* (L.) (Benamú *et al.*, 2013; El-Ghar & El-Sayed, 1992; Schläppi *et al.*, 2020). Cumulative toxicity ratings have been used by several authors successfully to investigate the long-term effects of multiple concurrent insecticides on natural enemies and pollinators, including studies in apple orchards (Marliac *et al.*, 2015; McKerchar *et al.*, 2020; Thomson & Hoffmann, 2006).

Based on the available spray records, cumulative toxicity ratings of the insecticides applied to the orchard blocks over the 20 years prior to the start of the experiment (using IOBC toxicity ratings estimated from available data; Tables 3.1 and 3.2) initially appear to explain the differences in WAA colony count between the blocks well. However, this ignores the fact that for a minimum of 7 years (prior to the experiment), all four blocks were treated with the same insecticide regime. In addition, spray data from 2012 to 2014 were missing, meaning that the blocks may have been treated the same way for as long as 10 years. The spray programmes since 2014 (applied to all blocks) included chlorpyrifos, spirotetramat, and flonicamid, all known to be effective against WAA (Beliën *et al.*, 2010; Kumar & Gupta, 2019; Manucci *et al.*, 2018; Schoevaerts *et al.*, 2011; Singh & Bhardwaj, 2018). The power of the cumulative toxicity scores to explain the differences in WAA colony counts relies mainly on differences in the quantity of chlorpyrifos sprays applied to the blocks in the years 2010 and 2011.

Chlorpyrifos is a broad-spectrum organophosphate insecticide, which is effective against WAA (Manucci *et al.*, 2018; Nicholas, Spooner-Hart & Vickers, 2003; Singh & Bhardwaj, 2018; Singh & Sharma, 2022) and has a half-life of 1 to 14 days on leaves, and will volatilise in open air (Racke, 1993). In soil, certain bacteria and fungi can biodegrade chlorpyrifos (Bhende *et al.*, 2022; Jaiswal *et al.*, 2017; Racke, 1993). However, the length of time chlorpyrifos remains in soils is extremely variable, with a half-life of up to 1576 days reported (Racke *et al.*, 1994), although most studies report values between 10 to 350 days (Aziz, 2018; Baskaran, Kookana & Naidu, 2003; Chai, Wong & Christian, 2013; Hua *et al.*, 2009; Liang *et al.*, 2011; Mosquera-Vivas *et al.*, 2016; Murray *et al.*, 2001; Neuwirthová *et al.*, 2018; Papadopoulou *et al.*, 2016; Racke, 1993). Once degraded, the main chlorpyrifos by-product, 3,5,6-trichloro-2-pyridinol, is also toxic to insects, and can have a longer half-life in soil than chlorpyrifos (Baskaran, Kookana & Naidu, 2003; Lewis *et al.*, 2016; Racke, 1993). Available data thus suggests it is unlikely that chlorpyrifos-related residues would still be present from 2010/2011 by the time of the study, but potentially primary chlorpyrifos metabolites could still have been present in the soil.

Woolly apple aphid reproduces rapidly, with up to 12 generations within a year in Europe (Molinari, 1986). In temperate climates it is understood that the majority of aboveground WAA in orchards die off over winter, reducing the population to those surviving below ground on the rootstock. The underground population survives winter and then individuals move upwards in spring to re-colonise the tree canopies (Beers, Cockfield & Gontijo, 2010; Hetherington, 2009; Heunis & Pringle, 2006; Theobald, 1921). Given this life cycle, WAA populations might be expected to recover well from non-systemic aerial insecticide applications, with the edaphic colonies providing a source of aphids to recolonise tree canopies each year. The likelihood of historical insecticide use as an explanation for differences between the blocks must also be weighed against other potential mechanisms not accounted for in this study. This includes microclimatic variations, differences in non-earwig enemy abundance, residual effects from non-insecticide anti-aphid treatments which may have been applied in previous experiments, or random variation in the starting populations of WAA. Furthermore, WAA colony counts were taken on different dates, so changes in climatic conditions could have influenced the results.

Unlike WAA, *F. auricularia* counts in this study were not significantly different between the blocks without artificial shelters, despite similar differences in cumulative toxicity rating between the blocks. Primarily, these were due to the use of chlorpyrifos and indoxacarb (Table A-6), both known to harm *F. auricularia* (Jana *et al.*, 2021; Nicholas & Thwaite, 2003; Shaw & Wallis, 2010; Vogt, Just & Grutzmacher, 2008). Under a conventional spray regime which included the broad-spectrum insecticide azinphos-methyl, the benefit of artificial shelters to *F. auricularia* appeared to be reduced (Nicholas, Spooner-Hart & Vickers, 2005). This was likely a result of direct mortality or avoidance, because WAA, suitable prey for *F. auricularia*, was more abundant in the azinphos-methyl treated blocks, suggesting use of the insecticide did not lead to a lack of suitable food.

However, Le Navenant *et al.* (2021) investigated the long-term effects of exposure to different levels of insecticides in *F. auricularia*. While not looking into the specific effects of different insecticides, the authors used toxicity rankings (Thomson & Hoffmann, 2006; Marliac *et al.*, 2015; McKerchar *et al.*, 2020) to measure the intensity of pesticide use in organic, IPM, and conventional orchards. In contrast to their earlier work (Suchail *et al.*, 2018), they found no significant differences in the weight of adult *F. auricularia* captured from the three different management types. The authors postulated that even if spraying disrupted *F. auricularia* feeding/growth earlier in the growing season, by the end of spraying in August *F. auricularia* in IPM or conventional orchards were able to feed enough to compensate for any weight loss caused by insecticide use. This may be easier for *F. auricularia* due to their highly varied omnivorous diet (Orpet *et al.*, 2019a; Phillips, 1981). They also showed that the offspring of *F. auricularia* from all three management types did not differ in weight or growth rate, when raised in the lab with *ad libitum* food. The only effect in the offspring was a shorter femur length in adult females whose parents had come from conventional orchards. This suggests that *F. auricularia* populations can recover rapidly from exposure to insecticides, and provides good evidence that the differences in historical spray regime which lead to the differences in cumulative toxicity rating for *F. auricularia* should be irrelevant to the earwig counts of this study.

The presence of artificial shelters was associated with significantly higher numbers of *F. auricularia* at night in apple trees. Few studies have tested how artificial shelters affect *F. auricularia* populations because few studies have monitored *F. auricularia* without the use of refuge traps, thus giving no point of comparison. Lamb (1975), and Lamb and Wellington (1975) conducted experiments on “wasteland”, consisting mainly of grasses, short herbs, and bare ground or gravel. In this environment they found evidence that artificial shelters helped maintain the *F. auricularia* population at a higher level, which they suggest may be from preventing predation by birds. There were also more *F. auricularia* living in areas with an abundance of natural shelter. The use of shelters in their studies appeared to be limited by food; when nearby food resources were exhausted, *F. auricularia* would disperse.

Carroll and Hoyt (1984) carried out night-time searches for *F. auricularia* in an orchard which had artificial shelters, and compared this to an orchard that did not. Nightly surveys revealed *F. auricularia* in the orchard with shelters, but no *F. auricularia* in the shelter-free orchard. However, unlike this study, the provisioning of shelters was accompanied by a release of laboratory-reared *F. auricularia* to increase the natural population, therefore obscuring any effect the shelters themselves may have had. Logan *et al.* (2007) tested the impact of artificial shelters in kiwifruit. They found that artificial shelters did not lead to increased numbers of *F. auricularia* foraging at night, nor did it appear that natural shelters and artificial shelters were ‘competing’ with each other for occupation by *F. auricularia*. The authors suggested that in kiwifruit vines, shelter was already abundant and not a limiting factor for *F. auricularia*. This possibly explains the difference in their findings and the results of this study, as comparisons between apple and pear orchards suggest that apple tree canopies do not always provide adequate natural shelters (Moerkens *et al.*, 2009).

To the author's knowledge, the only other study on the impact of artificial shelters on *F. auricularia* abundance in apples (without an accompanying release of *F. auricularia*) is that of Jana *et al.* (2021). Their findings appear to support the results of this study, in that significantly more *F. auricularia* were found in one of the treatments containing artificial shelters. However, of the two types of artificial shelter they tested, only one produced this effect. Interestingly, the shelter design which did not produce a significant effect was more similar to the design used in this study. It is also worth noting that the shelter-independent assessment method of Jana *et al.* (2021) was tap sampling during daytime, as opposed to the night-time searches employed in this study. If the artificial shelters in this study did improve the environment of Block 7 for *F. auricularia*, this could not have led to higher levels of reproduction during the period of the study due to the length of the *F. auricularia* lifecycle. Instead, reduced mortality could be responsible, or the population might have been concentrated onto the trees with artificial shelters, changing the population distribution without a change in *F. auricularia* abundance. However, despite this study appearing to show a positive effect of shelters on the number of *F. auricularia* in apple trees, similar to Logan *et al.* (2007), artificial shelters did not appear to enhance control of WAA.

While some studies have found *F. auricularia* provide effective control of WAA, often a high density of *F. auricularia* is required. Nicholas, Spooner-Hart and Vickers, (2005) found a minimum of five *F. auricularia* per tree was required, while Quarrell, Corkrey and Allen, (2017) suggested a minimum of 15, although this may depend on pest pressure and canopy density. Bischoff *et al.* (2024) investigated the interactions between *F. auricularia* population density, environmental complexity, and *F. auricularia* predation of WAA. They found more complex branches were harder for *F. auricularia* to search, and so WAA was more likely to survive in these complex environments. However, this effect could be overcome by increasing the *F. auricularia* population density. The block with the highest number of *F. auricularia* in this study had a mean of 1.9 *F. auricularia* per tree. Additionally, the artificial shelters in this study were present for only one growing season. Alins *et al.* (2023) showed that using artificial shelters along with *F. auricularia* releases to increase population numbers did lead to significant increases in WAA predation, but only after two consecutive years of release.

It is also worth noting that by measuring the number of WAA colonies with no consideration for colony size, this study only measured if *F. auricularia* were completely eliminating WAA colonies if/when they fed on them. Alins *et al.* (2023) also showed that colony size or length is often the best measure of the level of *F. auricularia* predation on WAA. Finally, the significant effect of block on WAA colonies in this study, and lack of replication, makes it difficult to draw conclusions on the interactions between *F. auricularia* and WAA.

3.5. Conclusions

These results suggest that in apple orchards the availability of shelter may be a limiting factor for *F. auricularia* populations. The addition of artificial shelters may help to increase or maintain the number of *F. auricularia* in an orchard, although augmentative releases may still be required for *F. auricularia* population densities to achieve the required level for control of WAA. Researchers should also exercise caution when using refuge traps to monitor *F. auricularia* population sizes in orchards and consider how potentially altering *F. auricularia* population dynamics might affect their research question(s). Finally, there were significant differences between the number of WAA colonies in the different blocks of this study. While cumulative toxicity scores based on the available years of spray records appear to match well with the WAA colony counts, the differences are difficult to explain with the available data.

4. Radio frequency identification mesocosm designs for the study of *Forficula auricularia* behaviour

4.1. Introduction

4.1.1. Radio frequency identification in entomology

Radio Frequency Identification (RFID) is a technology designed to detect and identify objects automatically and remotely (Landt, 2005; Ngai *et al.*, 2008). While a functioning RFID system consists of many parts, from an experimental design standpoint, the system can be simplified into two principal components: the tag, and the antenna.

In the study of animal ecology and behaviour, tags are attached to, or implanted into, study animals to enable detection and unique identification with the RFID system (Guillaume *et al.*, 2012). The antenna detects the tag within a defined distance, and records the time the tag is detected, termed a 'detection event', along with the identity of the tag/animal (Reynolds & Riley, 2002). Direction of movement in a single plane can also be recorded using 'directional readers' (a 'directional reader' is two antennas placed in sequence), which are often used to monitor centrally placed eusocial insects entering or exiting their nest (Ai & Takahashi, 2021). The tag is referred to as being 'read' during a detection event by the antenna (and attached computational system), which is used to detect and record the stored identity (a unique code) of the tag. The 'read range' or 'detection range' therefore both refer to the maximum distance a tag can be from the antenna and still be detected.

There are two main types of RFID system; using either active tags, or passive tags (Senadeera *et al.*, 2013). Active tags contain an internal battery, periodically transmitting a signal, which is detected by the antenna (Batsleer *et al.*, 2020; Reynolds & Riley, 2002). The need for a battery makes these tags larger and heavier than passive tags and means they cease to operate once the battery is depleted. The trade-off is that active tags have much longer read ranges than passive tags. The most powerful active RFID tags are detectable from space, allowing satellites to act as the antennas for these systems, with such systems typically being used to monitor large marine wildlife (Fedak *et al.*, 2002; Hazen *et al.*, 2017). In entomology, read ranges of hundreds of meters can be achieved with active RFID tags that are light enough to allow tagged insects to fly (Al Ansi, Aldryhim & Al Janobi, 2020; Beaudoin-Ollivier *et al.*, 2003; Chiari *et al.*, 2013; Hedin & Ranius, 2002; Kim *et al.*, 2019; Růžičková & Veselý, 2018; Thomaes *et al.*, 2018).

Passive RFID tags, in contrast, have no internal battery and instead power their activity using the electromagnetic field of the RFID antenna itself while in range (Reynolds & Riley, 2002). This allows them to be smaller and lighter than active tags, with operational lifetimes that can exceed the lifespan of the study species, at the cost of a significantly shorter detection range. In entomology studies, passive RFID systems often have a read range in the order of a few centimetres (Batsleer *et al.*, 2020). Pope *et al.* (2013) reported a read range of 14 cm, while Vinatier *et al.* (2010) reported a read range of 20 cm; these distances are indicative of the upper limit of passive RFID systems, in both cases from systems which use a mobile antenna. Read ranges of < 3 cm are common for fixed antennas (Alburaki, Madella & Corona, 2021; Decourtye *et al.*, 2011; Nunes-Silva *et al.*, 2020; Schneider *et al.*, 2012).

Radio frequency identification using active tags is also referred to as radio telemetry, while it is rare to see passive RFID referred to as such. In entomology, most RFID studies have been field-based. Active tags are typically paired with a mobile antenna; tagged insects are released and then relocated with the antenna to study their dispersal, as well as to observe the environmental microhabitats insects are occupying when re-detected (Chiari *et al.*, 2013). Vinatier *et al.* (2010) and Pope *et al.* (2013, 2015) used passive RFID antennas in a similar manner to radio telemetry. Vinatier *et al.* (2010) studied *Cosmopolites sordidus* (Germar), the banana weevil, while Pope *et al.* (2013, 2015) studied *Otiorhynchus sulcatus* (Fabricius), the vine weevil. In both cases these studies involved releasing tagged individuals and then relocating them with a mobile passive RFID antenna to study their dispersal distance and direction, alongside microhabitat preference. However, passive RFID systems are also employed with static/fixed antennas, both in insect and vertebrate ecology. By carefully considering antenna placement, researchers can use fixed antennas to study various insect behaviours.

Perhaps the most widespread use for fixed-antenna passive-RFID systems is the monitoring of honeybees (*Apis mellifera*, L.) or bumblebees (*Bombus* spp.) entering and exiting their nests (Batsleer *et al.*, 2020). The large colony size and fidelity to a nest over time makes them suitable for the use of passive RFID. Hundreds of bees can be tagged and monitored with the use of a single antenna by ensuring the nest has only one entrance/exit, thus maximising the tag-to-antenna ratio (which ensures the most data for the least cost; Gill & Raine, 2014). Flying worker bees are able to navigate to and from the nest and hence reliably return to the antenna repeatedly following foraging trips (Kheradmand & Nieh, 2019; Osborne *et al.*, 2013). This behaviour facilitates large, robust, dataset collection.

Fixed antennas are most powerful when they can be set up in locations which tagged insects must travel very near to (or through) as part of their 'daily routine', and which strongly demarcate a transition between different types of behaviour. Such behaviour transition points (BTPs) allow the RFID data-stream to split the daily routine of tagged individuals into time spent performing one set of behaviours or the other. Finding BTPs is therefore the greatest limitation of fixed-antenna RFID systems; without them, it is difficult to generate informative data on the study species. The entrance/exit of a shelter, or regular feeding site, are examples of this. If BTPs cannot be identified in the field, then artificial shelters or feeders can be constructed and deployed to allow the use of RFID monitoring in the natural environment. However, the use of enclosed experimental arenas, or mesocosms, can allow researchers to construct BTPs, and improve redetection rates in species that lack strong homing behaviour.

4.1.2. The potential of radio frequency identification enabled mesocosms

Most RFID studies have been completed under field conditions. However, RFID studies in mesocosms have also been completed on a wide range of taxa. In these mesocosm studies, fixed antennas may be used differently than previously described. For example:

Dyer *et al.* (2023) and Terlau *et al.* (2023) used an even distribution of RFID antennas across the floor of mesocosms, looking at the location and overall frequency of detections in different quadrants of the mesocosm. Terlau *et al.* (2023) used this to investigate the activity levels and occupation of different types of leaf litter by various insect species. Experimentally, this application of RFID is similar to technologies such as video tracking software (*e.g.* EthoVision®; Noldus Information Technology BV, Wageningen, Netherlands). It produces less-detailed information on the movement of individuals (in a 2D plane), but at a higher throughput, and without the need for an uninterrupted view of the insects, something which is critical when looking at the utilisation of leaf litter.

Ramesh *et al.* (2022, 2023) used RFID antennas to monitor the movement of *Gasterosteus aculeatus* (L.; three-spined sticklebacks) within and between a series of interconnected ponds. This experimental set-up allowed the researchers to compare different populations of three-spined sticklebacks and their movement behaviour at the scale of one pond as well as across the entire five-pond mesocosm. They showed that 'resident' fish which had been isolated by anthropogenic activity had reduced levels of between-pond movement when compared to an original 'migrant' population displaying ancestral behaviour.

Perhaps the most complicated and analytically-intensive series of RFID mesocosm studies are those completed by a research group at the University of Porto in Portugal (Beltrão, 2023; Beltrão, Gomes & Cardoso, 2022, 2023, Beltrão *et al.*, 2021, 2022; Gomes *et al.*, 2022, Gomes, Boogert & Cardoso, 2023; Saldanha *et al.*, 2024). These researchers used an aviary containing RFID-tagged common waxbills, with three types of antennas in the environment of the mesocosm. First was a directional reader used at the entrance/exit to a 'dormitory' consisting of boxes for the waxbills to hide in. Second were RFID antennas placed underneath long perches which overlooked the feeding boxes in the mesocosm. And finally, each feeding box itself contained an RFID antenna. Using these perches and feeding boxes, the researchers used the RFID data-stream to generate social networks of the waxbills within the mesocosm. This involved looking at overlap periods between pairs of birds detected at the same RFID antenna, as well as situations where one individual displaced another. Autonomous methods of gathering and computing observational data into social networks are of great interest in behavioural science. Over the course of several experiments, these researchers used their RFID-enabled mesocosm to show that changes in food availability led to increased aggression, more frequent, shorter foraging trips, and changes in how many waxbills flock together during foraging trips (Beltrão *et al.*, 2022; Gomes *et al.*, 2022). They demonstrated that bullying was used by more-dominant members of the waxbill social hierarchy as a low-risk method of advertising status, and that bullying was more likely when a bird of unknown social status was observing the interaction (Beltrão, Gomes & Cardoso, 2023). Ornamental plumage was the best predictor of social dominance, not size or weight; however, when plumage was experimentally manipulated, the social position of individuals did not change (Beltrão *et al.*, 2021; Gomes, Boogert & Cardoso, 2023). The social hierarchy was similarly resilient to prolonged absence of certain individuals. Finally, dietary tryptophan (an amino acid) enhancement led to increased aggression and feeding, counter to predictions (Saldanha *et al.*, 2024).

In insects, the simplest RFID-enabled mesocosm studies use a single non-directional antenna at the entrance to the nest of a eusocial insect (Stelzer, Stanewsky & Chittka, 2010; Tasman, Rands & Hodge, 2020; Yamanaka *et al.*, 2019). As the antenna cannot record the direction tagged insects are travelling, it is impossible to determine at any given time if an individual is inside or outside of the nest; a detection simply represents the transition between the two. These studies, therefore, use the number of detections to produce a metric of activity, with the assumption that when many insects are travelling in and out of the nest, this is with the main purpose of foraging to provision for the colony.

By using a directional reader in essentially the same experimental design framework, Molet *et al.* (2008) could determine when an individual bumblebee (*Bombus terrestris*) was outside the hive. They used this information to show that in response to either a simple or complex blend of artificial recruitment pheromone, the colony increased the collective foraging effort through the recruitment of a larger proportion of the workers; however, the duration that an individual worker spent foraging and resting did not change. This effect was stronger with the more complex blend, and when a colony's stores of honey were more depleted.

The RFID system used by Schneider *et al.* (2012) is a further increase in complexity, using two directional readers. These were placed at the colony entrance/exit, as well as at an artificial feeder, allowing the researchers to measure the time an individual honeybee took from leaving the hive to reach the feeder, the time spent at the feeder, and the time spent on the return flight from the feeder to the hive. They tested the effects of different doses of clothianidin and imidacloprid, administered manually and orally to honeybee workers caught at the artificial feeder. At higher doses of imidacloprid, they found decreases in the number of bees returning to the hive, short-term decreases in the number of trips to the feeder, increases in the duration of all three phases of a trip to the feeder. For higher doses of clothianidin, there was an increased duration spent at the feeder and the return flight, but no dose increased the duration of the flight to the feeder or the duration of periods between foraging bouts. It is important to note that this study was completed in the field; however, the design of the artificial feeder, and its placement seven meters from the colony entrance/exit, makes it very similar to a mesocosm study.

Russell *et al.* (2017) used a forked entry/exit tube, with a directional reader placed in each branch, to study the choices of individual bumblebees (*Bombus impatiens*, Cresson) to forage for either pollen or nectar. They found few individuals specialised in one resource across their lifetime, while 51% of bees specialised daily on one resource. Additionally, overall foraging effort was highly skewed, with many bees contributing little while a small number completed a disproportionately higher number of foraging trips.

Avila *et al.* (2022) used RFID-enabled artificial flowers of different colours, which released either a sucrose solution or water upon detecting a tagged *B. impatiens*, to test how streptomycin (an antibacterial chemical) affected the learning ability of bumblebees. They found exposure to streptomycin did not reduce the overall number of trips bees made to the artificial flowers, but did reduce the number of trips they made to the flower which rewarded them with sucrose (as compared with control bees). This, in combination with other learning assays, suggested that dietary streptomycin reduced the ability of bees to learn and forage. It is worth noting that of these studies using RFID systems in mesocosms (with the mentioned caveat for Schneider *et al.* (2012)), all apart from Yamanaka *et al.* (2019) studied either bumblebees or honeybees.

Forficula auricularia is not an ideal study species for RFID in the field. While *F. auricularia* readily uses artificial shelters, which would provide a good BTP, previous research suggests individuals have poor navigational abilities, and no fidelity for using the same refuge repeatedly (Lamb, 1975; Lamb & Wellington, 1975; Phillips, 1981). They do not appear to be highly selective when choosing shelters, and in most environments where an RFID-enabled shelter might be deployed, there would probably be natural refuges that tagged *F. auricularia* might use instead (Gobin, *et al.,* 2008b; Phillips, 1981). All of this means that while it may be possible to deploy RFID-enabled artificial shelters in the field and get some detection/redetection of tagged *F. auricularia*, a high number of antennas, and a very large number of tagged individuals would be required to generate a robust dataset. While foraging behaviour is poorly understood, all evidence suggests *F. auricularia* is highly polyphagous, feeding on a variety of animal and plant food sources, with no tendency to navigate back to food sources repeatedly over time (although see below; Beall, 1932; Jiang & Kajimura, 2020; Orpet *et al.*, 2019a; Phillips, 1981). Therefore, it seems impossible to identify a location in the field where an RFID antenna could be deployed that would consistently redetect tagged and released *F. auricularia* in high enough numbers to justify the cost of RFID tracking.

However, *F. auricularia* show strong spatial fidelity after mating. Females and males excavate a brood chamber, the female lays a clutch of eggs, and will then remain in the chamber to care for the eggs and the offspring once they emerge (after driving the male off; Boos *et al.*, 2014; Mas, Haynes & Kölliker, 2009). During most of this period, it is understood that the female does not feed, remaining within the brood chamber and therefore making RFID monitoring purposeless. After the offspring emerge, the female will sometimes forage for food and return to feed their young (in other cases they will leave to lay a second clutch of eggs; Mas, Haynes & Kölliker, 2009; Staerkle & Kölliker, 2008; Van Meyel, Devers & Meunier, 2019, 2021). During this time, an antenna placed at the entrance to the brood chamber could be used to study the foraging of the mother if she were tagged. However, such a setup uses a single tagged individual per antenna and is thus extremely costly for the volume of data acquired. This stage, where the mother earwig is leaving the brood chamber to forage and return with food for her young, also only lasts for two weeks (Kölliker, 2007; Tourneur & Meunier, 2020; Van Meyel, Devers & Meunier, 2019).

While *F. auricularia* is not an ideal subject for field-based RFID studies, remote monitoring could assist in the study of their behaviour. As mentioned, *F. auricularia* behaviour is poorly understood. Almost all field research on *F. auricularia* relies on observing and studying individuals during the day, the dormant part of *F. auricularia*'s daily routine, with the insects being collected for observation by refuge trapping. Attempts at tracking and observing *F. auricularia* during its active phase at night have proved challenging; they will stop moving when subject to the light of a torch, and attempts by the author as well as those of Lamb (1975) to use either fluorescent powder or paint and a UV torch have had little success. The only behaviour well-studied in the laboratory is maternal brood care. Much of the foundational knowledge about earwig foraging comes primarily from laboratory-based studies conducted by Lamb and Wellington in the 1970s (Lamb, 1975; Lamb & Wellington, 1975), although gut content analysis has provided information on what *F. auricularia* is feeding on in the field (Orpet *et al.*, 2019a; Phillips, 1981; Romeu-Dalmau, Piñol & Agustí, 2012). How often earwigs forage, whether they will leave and return to shelters multiple times in the night, and how or if they prioritise food sources of different qualities and distances from a shelter, is all unknown.

While RFID tagging is a well-established method in invertebrate ecology, comparatively little attention has been paid to the effects of tagging on insects. Batsleer *et al.* (2020) completed a systematic review highlighting the lack of clear reporting of basic information such as tag:body mass ratios or the glue used in RFID studies, with empirical testing of the effects of tagging urgently needing more attention. Their review focused mainly on the importance of tag weight; however, the choice of glue can have a substantial impact on studied insects (Boiteau *et al.*, 2009, 2010; Pope *et al.*, 2015; Switzer & Combes, 2016; Toppa *et al.*, 2020). Cyanoacrylate-based superglues are often selected due to their strong bonding and fast drying, despite studies showing they can be damaging or even lethal to various insect species (Boiteau *et al.*, 2009; Pope *et al.*, 2015; Toppa *et al.*, 2020).

As there have been no published studies using RFID tracking on *F. auricularia*, this study aimed to:

1. Develop a method for tagging earwigs
2. Test glues both independently and in combination with tags for potential detrimental effects of tagging on earwigs
3. Test glues for their effectiveness in attaching RFID tags to earwigs
4. Design a prototype mesocosm which might be able to generate ecologically relevant information on *F. auricularia* behaviour in a lab setting

4.2. Methods

Forficula auricularia 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 *F. auricularia* 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 *F. auricularia* 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.

4.2.1. Glue testing

Six glues were tested (Table 4.1), either with or without passive RFID tags, giving 12 experimental treatments and one control treatment. Ten *F. auricularia* (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 × 1.6 × 1.3 mm in size. Three *F. auricularia* escaped during the experiment; data from them was discarded. Each *F. auricularia* was placed individually in a tube and CO_2 applied to the tube using a lance until the *F. auricularia* became motionless. The *F. auricularia* were left in the CO_2-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 earwig, or applied first to a piece of waxed paper, and then transferred to the elytra of the earwig 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 (± standard deviation). The platform the *F. auricularia* were placed on was covered in foam. The stem of the platform the *F. auricularia* were placed on extended beyond the end of this cylinder. To hold the *F. auricularia* 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 4.1). This meant the weight of the cylinder was supported by the earwig 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 *F. auricularia*.

Table 4.1. 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	Cyanoacrylate	Gorilla Glue Europe Limited, 26 Eaton Avenue, Buckshaw Village, Chorley, England, PR7 7NA

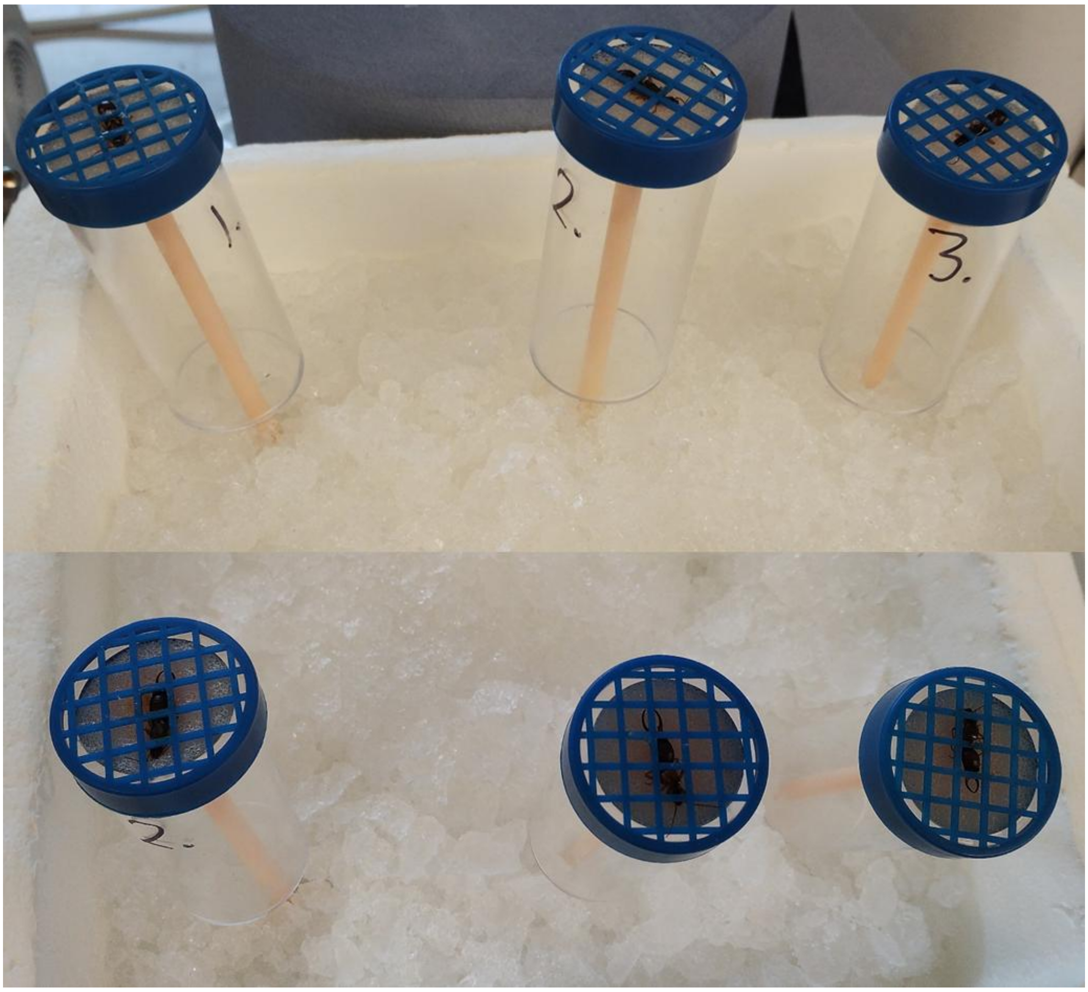

Figure 4.1. Two images showing anesthetised *Forficula auricularia* which have been placed into a bee marking cage for the application of glue (with or without a tag) onto their elytra. The bee marking cages were placed in ice to keep them upright while allowing the weight of the mesh and attached plastic 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 anesthetisation.

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, *F. auricularia* were provided with one half of a prototype Wignest™ (Russell IPM Ltd., Flintshire, UK). This was to avoid providing *F. auricularia* 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 *F. auricularia* 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 anesthetised with CO_2, as before, to remove the tag. Starting at 17:00 each day (typically requiring 40 minutes), and 2 hours after treatment, each *F. auricularia* 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, *F. auricularia* 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 *F. auricularia* had escaped the sample tube by successfully climbing the vertical surface. Any *F. auricularia* 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.

4.2.2. 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 Akiake 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.

4.2.3. Prototype radio frequency identification mesocosm

To test the practicality of using fixed-antenna passive RFID tagging to collect behavioural data on *F. auricularia*, two prototype mesocosms were designed. Both consisted of a large Perspex box (210 x 105 mm at base, 227 x 120 mm at top, 85 mm vertical height, lid attached; hereafter referred to as the 'large box') and a small Perspex box (same dimensions as used for the glues testing; hereafter referred to as the 'small box'), which were connected via a 70 mm length of plastic tubing. The tubing was fixed in place using thermoplastic glue. Both the small box and large box had holes in them covered in fine mesh to provide ventilation. In one mesocosm, Fisherbrand™ Polyvinyl chloride (PVC) Colourless Tubing (outer diameter: 14 mm, inner diameter: 10 mm) was used, in the other Fisherbrand™ Silicone Tubing (outer diameter: 17.5 mm, inner diameter: 12.5 mm). In each mesocosm, two water feeders were provided, one in each box. The two halves of a prototype Wignest were provided as shelter in the large box. Food was provided as in the glues testing, but was only placed in the small box. Figure 4.2 shows a diagram and photos of the mesocosms.

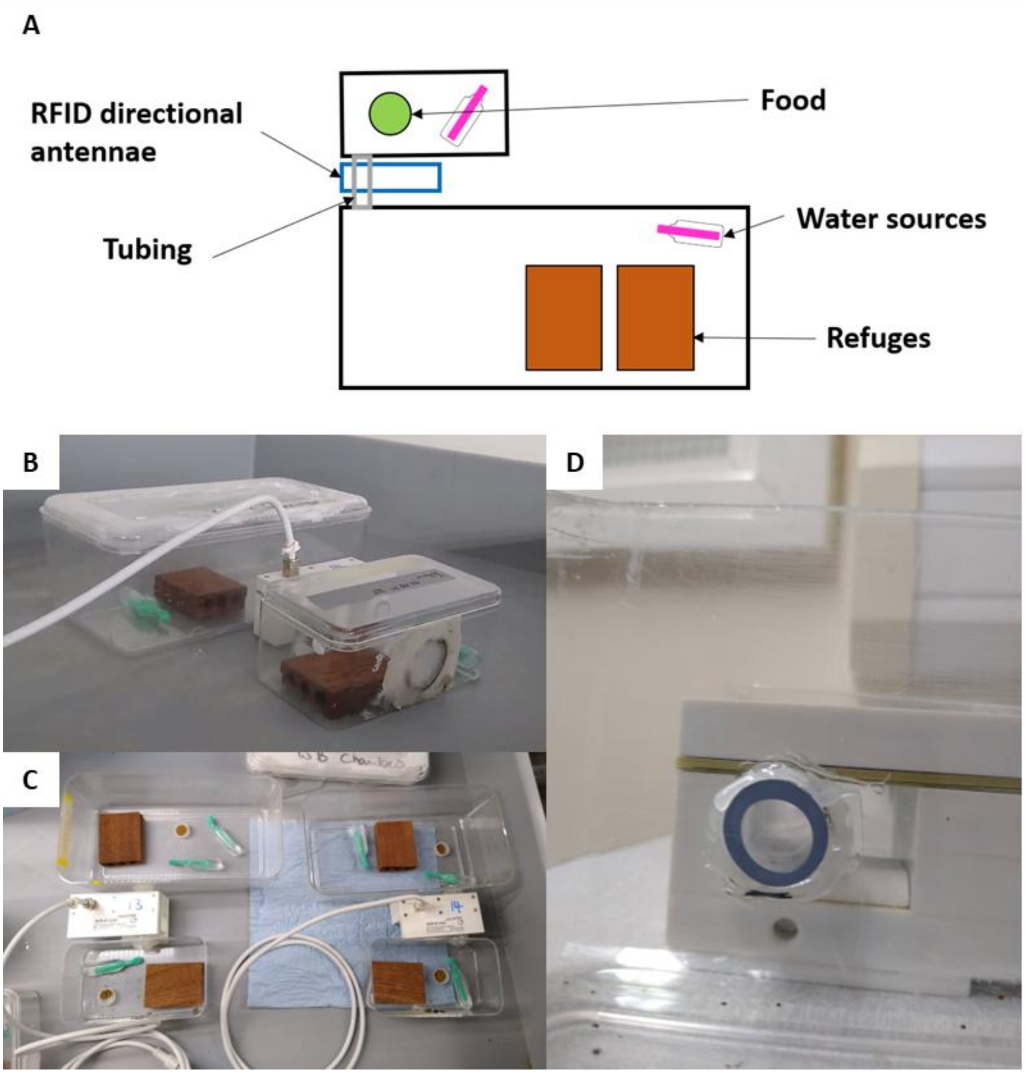

Figure 4.2. A) A labelled diagram showing the experimental set-up of the prototype RFID mesocosms used in the test. Not to scale. B) A photograph showing the PVC mesocosm in use during a test carried out prior to the one discussed here. The arrangement of shelters and food in the image is different than that used in this experiment. C) A photograph showing both mesocosms without the lids on. The mesocosm on the left is the silicone one, on the right is the PVC one. The arrangement of shelters and food in the image is different than that used in this experiment. D) A photograph showing the PVC tubing running through an RFID reader.

The mesocosms were fitted with an iID®HIVE Entrance Reader AEB-03.C2D, a directional RFID reader (two antennas placed in sequence) designed to work with the mic3 Q1.6 passive tags used in the glues testing. The plastic tubing connecting the boxes of each mesocosm was threaded through the aperture in each reader. The aperture is designed to encompass the read range of the two antennas that make up the reader. Any tagged insect which travelled through the tube would thus be detected by the reader. The plastic tubing did not interfere with the readers' ability to detect RFID tags. The two readers were connected to an iID®BEE controller CCO-01DC, which recorded the data from the readers, and processed it using iID®Data Capture Software BEEscience v. 01.06. The readers, controller, and software are all products of Microsensys GmbH, Erfurt, Germany. The controller was set to record detections every 15 seconds.

Forficula auricularia were captured for this experiment by hand from strawberry tunnels at Niab, East Malling, UK. These were kept in the same type of box as the large box of the mesocosms, with shelter, food, and water provided as in the mesocosms and glues testing. This population was kept in a temperature-controlled room set to 25 °C, with a 16:8 Light:Dark cycle (hours). A datalogger was placed in the large box of the PVC mesocosm at 13:05 on 2022.04.08 and took temperature and humidity measurements every hour (Table 4.2).

Table 4.2. Summary statistics from a datalogger placed in the PVC mesocosm for part of the experiment. Max = maximum. Min = minimum. Standard dev. = standard deviation. Readings were taken hourly. *N* = 323.

Statistic	Temp (°C)	Humidity (%)
Max	22	77
Min	17	41.5
Range	5	35.5
Mean	19.02	62.76
Standard dev.	0.99	7.28

Individual earwigs were selected for the RFID mesocosm test haphazardly from those captured. All individuals were adult. No attention was paid to the sex of individuals. Tags were applied to the *F. auricularia* as in the glues testing, with the following modifications. Araldite glue was used for all *F. auricularia*, and tags were applied to all *F. auricularia*; there was no glue-only treatment. After being anesthetised with CO_2, the *F. auricularia* were placed in a hand-made device (Earwig Immobilisation Ring, EIR) rather than a bee marking cage. At the time, bee marking cages had not been purchased, and the EIR were designed to have a smaller aperture size in the hopes that this would improve the consistency of immobilisation. These were constructed from wooden curtain rings (diameter 55 mm), with holes drilled through, and fishing line threaded through and tightened to create a grid. Due to the hand-made nature, the size and shape of the holes in the grid varied, but were typically 4 mm. Two EIRs were made. Once unconscious, *F. auricularia* were placed on a sponge, the EIR was lowered onto them, the glue and tag were applied to the elytra, and then either five or six plastic Petri dishes were balanced on the EIR to provide additional weight. The total weight of EIR 1 and the Petri dishes was 49.1 g, for EIR 2 and the Petri dishes it was 38.7 g. As with the bee marking cages used in glues testing, if an *F. auricularia* came to consciousness and began moving during the scheduled 20 minutes of time spent in the EIR, it was immediately removed. Once tagged, the *F. auricularia* were placed in a box with no heavy objects as in the glue testing. They were transferred the first day after tagging to a box which contained half of a Wignest as shelter. The second day after tagging, they were then transferred to one of the two prototype mesocosms.

The RFID mesocosm test began on 2022.03.14, and ended on 2022.04.21, a period of 38 days. An initial cohort of 10 *F. auricularia* were introduced to the mesocosms, five in the PVC mesocosm and five in the silicone mesocosm. Throughout the experiment, three *F. auricularia* detached their tags, and five died. An additional 10 tagged *F. auricularia* were also introduced at various points during the experiment. Daily observations were made of the mesocosms during the experiment, although there were several gaps in observations, with the longest lasting 11 days. Each time, the number of *F. auricularia*: 1) in the mesocosm 2) in the large box 3) in the small box 4) in the tunnel 5) which had detached their tag, and 6) which had died, were recorded. These observations, including the dates on which all new *F. auricularia* were introduced to each mesocosm, are available in Table A-7. All *F. auricularia* were released into the small box of their respective mesocosm. Food and water were changed approximately twice a week. Other than the addition of food and water, and the disturbance required to check the occupation of the refuge and plastic tunnel, *F. auricularia* were not handled once released into the mesocosms.

4.2.4. Radio frequency identification enabled mesocosm statistical analyses

The text files produced by the BEEscience software were converted to Microsoft Excel files, and then analysed using R and the following packages: openxlsx (Schauberger & Walker, 2025), dplyr (Wickham *et al.,* 2023), ggplot2 (Wickham, 2009), readr (Wickham, Hester & Bryan, 2024), lubridate (Grolemund & Wickham, 2011), purrr (Wickham & Henry, 2025) and scales (Wickham, Pedersen & Seidel, 2023). The data from each tag was separated and analysed separately. Only summary statistics were generated. Given that individual *F. auricularia* were in the mesocosms for different numbers of days, a minimum number of earwig-days (433) was calculated. As observations were not taken every day during the experiment, the earwig-days minimum was calculated by assuming that any detachments or deaths that occurred during periods where the mesocosms were not observed for multiple days occurred on the earliest possible day (thus giving the lowest possible occupation of the mesocosms on the unobserved days). This number (433) can be thought of as a 'target' that would have been reached if every individual in the mesocosms had been detected at least once a day. Because *F. auricularia* individuals could not be distinguished by eye, the number of *F. auricularia* which passed from the small box into the large box was estimated by assuming that there was no substitution of individuals (*i.e.* that once an individual moved in the large box it never moved back into the small box) and is thus a minimum value. Note that the observations and RFID data are congruent with this assumption (*e.g.* the number of *F. auricularia* observed in the large box only decreased when individuals were removed due to tag detachment or death).

4.3. Results

4.3.1. Glue testing

4.3.1.1. 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 4.3). 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 earwig treated with Gorilla gel died (out of 10), and none of the 10 earwigs treated with Gorilla glue (and a tag) died.

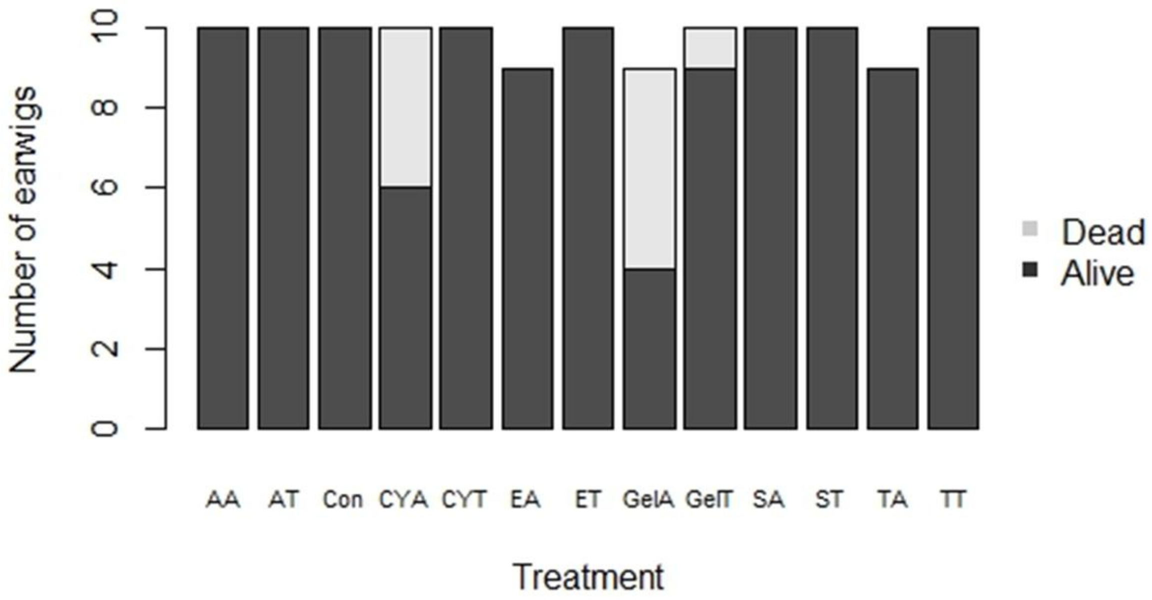

Figure 4.3. A bar chart showing the number of *Forficula auricularia* which either survived or died following a given treatment during a fourteen-day experiment. The treatment codes stand for the following: AA = Araldite alone, AT = Araldite with tag, Con = Control, CYA = Gorilla glue alone, CYT = Gorilla 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.

4.3.1.2. 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 4.4). 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 4.5 shows that the model predicted Araldite and shellac to perform better as time spent in the bee marking cage trended towards 0.

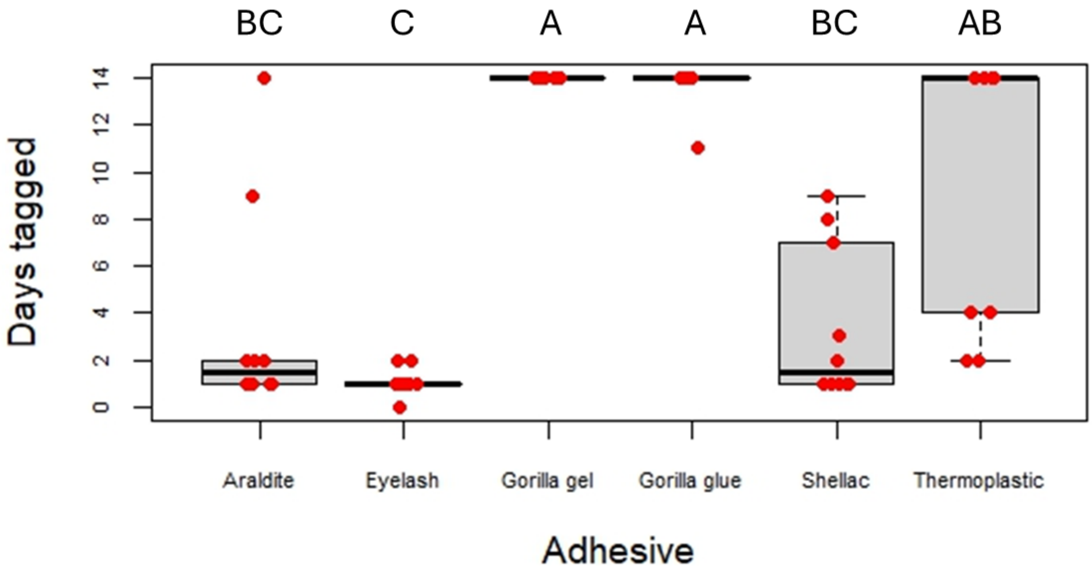

Figure 4.4. A boxplot showing the number of days tags remained attached to *Forficula auricularia* using various glues. The datapoints are superimposed in red. Treatments which do not share a letter are significantly different ($p \leq 0.05$). N = 10 for all treatments apart from Gorilla gel where N = 9. The experiment ended after fourteen days.

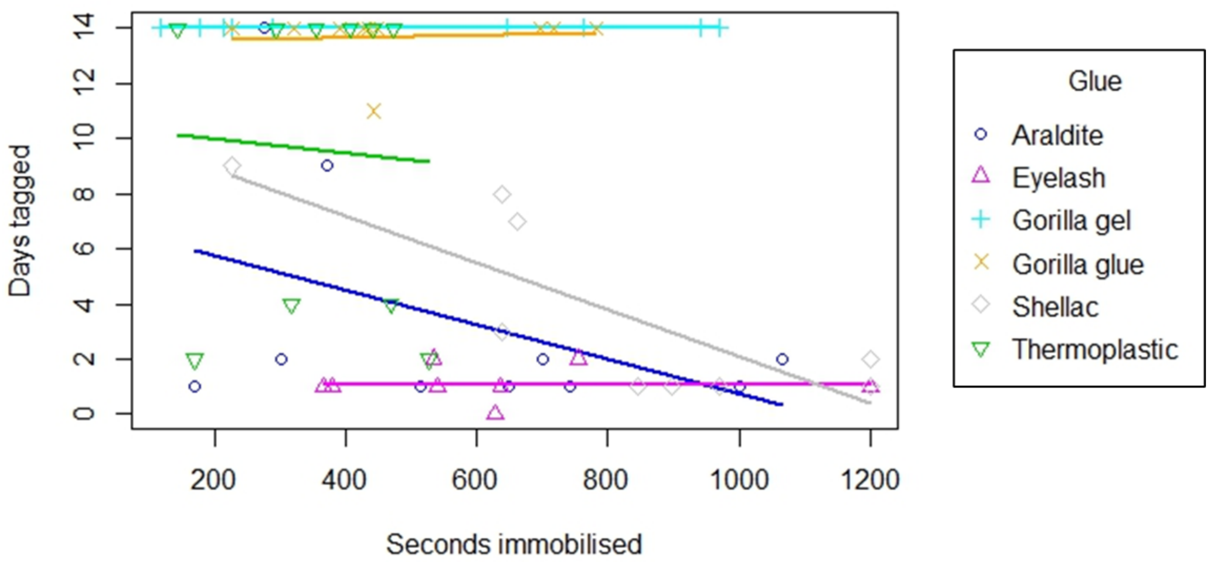

Figure 4.5. A scatterplot showing the predicted relationship between the time spent immobilised in a bee marking cage and the number of days a tag remained attached to a *Forficula auricularia* for different glues, based on a negative binomial generalized linear model. N = 10 for all treatments apart from Gorilla gel where N = 9. The experiment ended after fourteen days.

4.3.2. Prototype radio frequency identification mesocosm

During the 38 days of the mesocosm test, a total of 27,662 individual detections were made. The vast majority of these were detections of a single *F. auricularia*, Earwig 9. Indeed, Earwig 9 was detected 27,618 times, making up 99.8% of the total detections, and thus being detected 628 times more than all other *F. auricularia* combined. Earwig 9 was first detected at 2022.03.22, 23:44:54, and it was last detected at 2022.04.08, 14:42:40; between these a total of 16 days 14 hours 57 minutes and 46 seconds elapsed. Most detections of Earwig 9 occurred in periods of continuous detection, where the RFID reader repeatedly detected Earwig 9 with only short gaps between detections. Periods where Earwig 9 was continuously detected with no gap longer than 20 minutes made up a total of 5 days 2 hours 29 minutes and 37 seconds. Between its first and last detection, there were 61 periods during which Earwig 9 was not detected for longer than 20 minutes, these totalled 11 days 12 hours 28 minutes and 09 seconds. The period from Earwig 9's first to last detection is displayed in Figure 4.6, with the x axis representing the number of times Earwig 9 was detected within 20 minutes (the 15-second cycle on the RFID controller means the maximum is 80). After last being detected, there was a further 12 days at the end of the experiment during which no *F. auricularia*, including Earwig 9, were detected.

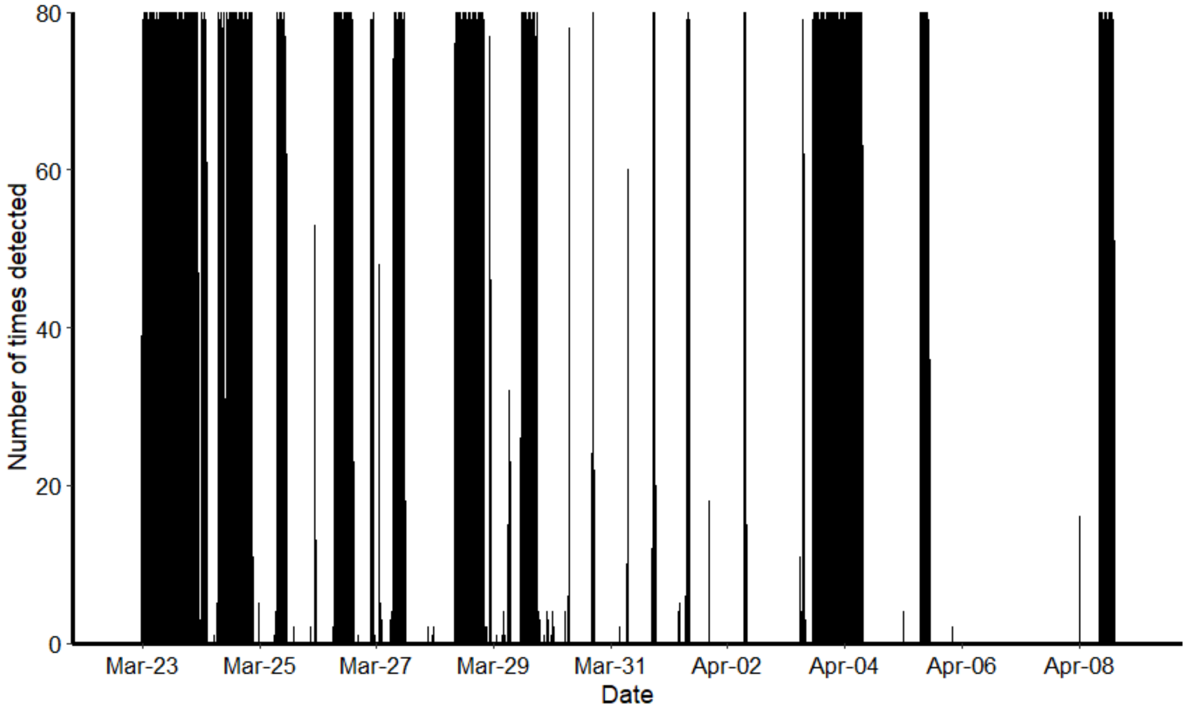

Figure 4.6. A timeline of the frequency that Earwig 9 was detected across 1,197 20-minute intervals. The maximum number of detections within 20 minutes was 80. Earwig 9 was first detected at 2022.03.22 23:44:54, and last detected at 2022.04.08 14:42:40.

There were 10 other *F. auricularia* that were detected by the RFID readers (11 total including Earwig 9). All other *F. auricularia* that were detected during the experiment were detected on only a single day, with the longest period between first and last detection being 5 minutes and 18 seconds (Table 4.3). Four of the detected *F. auricularia* were in the mesocosm with the PVC connecting tube, the other seven were in the mesocosm with the silicone tube.

There were nine *F. auricularia* that were never detected by the RFID readers. When standardised using earwig-days, there were 24 earwig-days on which at least one detection occurred, out of total of 433. However, 14 of these earwig-day detections come from Earwig 9, with the other 10 individuals detected each contributing a single earwig-day. A minimum of 10 *F. auricularia* were observed to have moved from the small box the large box during the experiment. There were nine occasions on which an *F. auricularia* was inside the tunnel during inspection: one of these was in the PVC mesocosm, the other eight were in the silicone mesocosm. There were days on which an *F. auricularia* was observed inside the tunnel, but no detection was made by the RFID system. Only a single *F. auricularia* was observed occupying a given tunnel at any time. Although the RFID readers were directional, there were multiple occasions on which the same individual was detected moving in the same direction twice in a row, indicating a misread.

Table 4.3. Summary data on the 11 *F. auricularia* which were detected during the course of the 38-day experiment.

Name	Material	Date detected	*N* detections	Time between first and last detection
Earwig 1	Silicone	2022.03.29	19	5m 18s
Earwig 2	PVC	2022.03.15	1	N.A.
Earwig 3	Silicone	2022.03.18	7	3m 1s
Earwig 4	PVC	2022.03.14	2	15s
Earwig 5	Silicone	2022.03.30	4	1m
Earwig 6	PVC	2022.03.22	2	15s
Earwig 7	PVC	2022.03.16	1	N.A.
Earwig 8	Silicone	2022.03.15	4	1m 45s
Earwig 9	Silicone	Multiple	27618	16d 14h 57m 46s
Earwig 10	Silicone	2022.03.21	2	16s
Earwig 11	Silicone	2022.03.17	2	46s

4.4. Discussion

This study showed there were significant differences between the effectiveness and toxicity of various glues for attaching RFID tags to *F. auricularia*. In terms of tag retention, the two cyanoacrylates (Gorilla glue and Gorilla gel) tested were the most effective, as only a single cyanoacrylate-attached tag became detached over the course of the 14 days. Cyanoacrylates are the most-used glues for RFID studies on insects, due to their fast drying times and strong bonds, and most papers report no ill effects of tagging with cyanoacrylate glues. However, this study and others have found them to be harmful to some species of insect. While pairwise comparisons were not significant between the treatments in this study, there is some evidence for an effect of cyanoacrylates on the mortality data. The only earwigs to die during the experiment were in the cyanoacrylate treatments, and when Gorilla glue and Gorilla gel were tested without tags, approximately half of the treated earwigs died during the 14-day experiment. These results provide evidence to suggest that cyanoacrylate glues are toxic to *F. auricularia*. Boiteau *et al.* (2009) did not find significant increases in *Conotrachelus nenuphar* (Habst; plum curculio) and *Leptinotarsa decemlineata* (Say; Colorado potato beetle) mortality when cyanoacrylates were applied to them, but *Diabrotica virgifera virgifera* (LeConte; Western corn rootworm) and *Diabrotica barberi* (Smith and

Lawrence; Northern corn rootworm) were rapidly killed by three different cyanoacrylates. Boiteau *et al.* (2010) found a fourth cyanoacrylate was similarly lethal to western corn rootworm, and corn rootworm walking speed increased with tagging, which they speculated may be due to “latent lethal effect” of the glue (among other theories). Kirkpatrick *et al.* (2019) state that the three cyanoacrylate glues used by Lee *et al.* (2013) lead nymphal *Halyomorpha halys* (Stål; brown marmorated stinkbug) to become immediately moribund or dead. This result does not appear to be published, and Lee *et al.* (2013) found no significant effects of the glues on adult *H. halys*, while Kirkpatrick *et al.* (2019) tested 4 different cyanoacrylates on nymphal *H. halys* and did not find a significant increase in mortality for any of them. Pope *et al.* (2015) compared thermoplastic glue to a cyanoacrylate for tagging vine weevil and found the cyanoacrylate significantly increased mortality when compared to thermoplastic glue and control weevils. In addition, both glues negatively impacted the mobility of tagged weevils, but the cyanoacrylate was significantly worse than thermoplastic glue in terms of its effect on both horizontal and vertical movement. Toppa *et al.* (2020) compared a cyanoacrylate to shellac, both alone and with RFID tags, on the stingless bee *Melipona quadrifasciata* (le Peletier). There was evidence that the cyanoacrylate and tag had cumulative negative effects on the bees; cyanoacrylate with a tag led to significantly increased mortality, while cyanoacrylate alone, and shellac with or without a tag, all had similar survival to control bees. Cyanoacrylate, either alone or in combination with a tag, led to disruption of the flight muscle tissue, while tagging led to altered glycogen storage in the muscles, which was more pronounced for tags attached with cyanoacrylate (though the glue alone did not produce this effect).

While previous research supports the finding that cyanoacrylates might be toxic to *F. auricularia*, it might be expected that the treatments combining the stress of the glues with tags would result in higher levels of mortality than the glue alone. To our knowledge, Boiteau *et al.* (2010) and Toppa *et al.* (2020) are the only other studies to directly compare glue-alone and glue-with-tag treatments; however, their results are contradictory to our own. Boiteau *et al.* (2010) only compared the glue-alone to the glue-with-tag for one of the three study species, *C. nenuphar*. They state, for their vertical movement test, only “The glue alone did not have a significant impact.”, but do not discuss this result further. However, the comparison between glue-alone and glue-with-tag was not clear. In both their horizontal and vertical movement tests, glue-alone treatments were not significantly different from control treatments, but neither were they significantly different from the glue-with-tag treatments which did have a significant effect. These results, then, are mixed, but seem to suggest that the glue-alone may have had some impact on plum curculio, while glue-with-tag had a stronger impact.

The results of Toppa *et al.* (2020), unlike those of Boiteau *et al.* (2010) and our own, clearly demonstrate an effect from both glue-alone and glue-with-tag treatments, and that the toxicity of a cyanoacrylate combined with the weight of a tag had a greater impact on *M. quadrifasciata* than either a cyanoacrylate-alone or a tag applied with a non-toxic glue. In our study, while approximately half of *F. auricularia* treated with cyanoacrylate glue-alone died, only a single earwig treated with cyanoacrylate-with-a-tag was killed. Again, the lack of significant pairwise comparisons must be considered; however, this appears to suggest that the application of a tag somehow ameliorated the toxic effect of the cyanoacrylates on *F. auricularia*. This is difficult to explain and may stem from a lack of replication. Perhaps the increased handling time required to apply a tag to the earwigs’ elytra, or the spreading of the glue laterally, in some way worked to reduce the quantity of cyanoacrylate which is absorbed by *F. auricularia*. While effort was taken to ensure a similar volume of glue was applied each time, it is also possible that a different quantity of glue was applied when in combination with a tag. However, it would be expected that more glue would be used when attempting to attach a tag; in glue-alone there was no mechanical requirement placed on the glue so there was no minimum volume required for correct adhesion.

When considering tag retention and mortality/toxicity, thermoplastic glue appears to be the best choice of glue for the RFID tagging of earwigs. While few *F. auricularia* were killed by cyanoacrylate-with-tag, it would be best practice to avoid exposing earwigs to cyanoacrylates when studying their behaviour. Video A-1 is a video of an earwig that has been tagged with Araldite glue and appears to show a deliberate attempt to scrape the tag off using one of the water feeders. This suggests that even in the absence of strong toxic effects from glue (note that Araldite glue may still have been toxic to some extent), the weight and bulk of RFID tagging can be disruptive to *F. auricularia* behaviour. It is unclear if tag-scraping behaviour is a short-term response, with individuals eventually becoming acclimated to the presence of tags over time, or if this behaviour persists for the duration of tagging. It was not directly observed again, although detached tags were frequently found on hard edges inside the containers earwigs were housed in for the experiment. Similar efforts to remove RFID tags have been observed for other species (Barlow, O'Neill & Pavlik, 2019; Boiteau *et al.*, 2009; Hagen, Wikelski & Kissling, 2011; Koenig & Petersen, 2022; Toppa *et al.*, 2020). Thermoplastic glue with-tagging was the heaviest treatment in this study, and the glue residue on the elytra of the earwigs was visibly bulkier than for other glues. This drawback could be compensated for by using a more precise hot-glue gun.

Another area of the methodology which might be improved is the immobilisation of the earwigs. In preliminary experiments, CO_2 exposure was more consistent and less harmful to *F. auricularia* than chilling in a -15 °C freezer. However, the bee marking cage was not an ideal solution for holding the earwigs in place once unconscious and the EIRs were no more effective. A uniform degree of force that can be applied to hold *F. auricularia* of all sizes has not been found. There appears to be considerable overlap between weights that will crush the abdomen of a large female and from which smaller and flatter individuals can escape from. In practice this meant erring on the side of lighter weights, which do not consistently immobilise *F. auricularia* once applied. If an *F. auricularia* recovered consciousness while in a bee marking cage, it was immediately removed from the bee marking cage, as their struggling can often detach the tag on the grid of the cage. An alternative method of applying force to hold *F. auricularia* still, one which applies more uniformly across the entire body of the earwig, might provide a more consistent method to immobilise *F. auricularia* indefinitely, and hopefully improve the successful tagging rate as a result. Pope *et al.* (2015) immobilised insects by pressing them into Blue-tack® (Bostik Ltd., Leicestershire, UK) putty, a similar method could be investigated for use on *F. auricularia*. It is unclear why the time spent in the bee marking cages in this study appeared to be negatively correlated with the number of days a tag attached using araldite or shellac remained attached. It may feasibly have been more effective not to immobilise *F. auricularia* at all after the application of the treatments.

The tag placement on the centre of the elytra was reasoned to have the least impact on *F. auricularia* behaviour, whilst also providing the best chance of success for the tagging procedure. While *F. auricularia* does possess functional wings, it is extremely rare for these wings to be used, to the point that earwigs may be effectively excluded from tree canopies through the use of sticky bands around the trunk (Nicholas, Spooner-Hart & Vickers, 2005). Instead, the elytra and mesothorax represents the only flat, rigid body segment large enough to support a tag without impinging on the earwig's ability to flex its body segments. Attachment to the pronotum or abdominal segments would necessitate the application of glue across multiple segments, effectively fusing them. Applying glue across segments might also allow the glue to penetrate more easily into the body, increasing the severity of any toxic effects. Attachment to the elytra has the additional benefit of placing the tag between the contact points of all six feet, and therefore hopefully having a minimal impact on the centre of balance.

The design of the RIFD mesocosms was envisioned to split the daily routine into two sections: time spent foraging *vs.* time spent sheltering. For this reason, all the food was placed in the small box, while the shelters were provided in the large box, with tagged *F. auricularia* forced to travel between the two through the tube (the BTP) and thus be detected by the RFID reader. For the tube to act as a true BTP, several assumptions must be met. Firstly, it is important that the only location where *F. auricularia* can shelter is in the large box. The half-Wignest in the large box should, in theory have been the only location in the mesocosms which provided darkness during the 16 hours of light each day, and a tight space which satisfied the positive thigmotaxis of *F. auricularia*. However, the diameter of the connecting tubes was small enough that this appeared to satisfy the desire for tight spaces, as *F. auricularia* were observed occupying the tube on multiple occasions (this behaviour was also observed in other live tests of the RFID mesocosm not presented here). In addition to being a tight space, the design of the RFID readers meant that the tube was also shaded from the light, further increasing the suitability of the tube as an alternative refuge to the half-Wignest. This appears to be the reason for the enormous volume of data generated by Earwig 9. Also, while it was impossible for *F. auricularia* to feed in the large box, it is entirely possible that foraging took place in the large box and *F. auricularia* were simply unable to find the tube and use it to pass back into the small box when they wished to feed. The author observed that it was common for *F. auricularia* to move around the perimeter of whichever box they were in, in contact with the floor and one side of the box. While they were perfectly capable of climbing the walls of the box, this was not attempted frequently, and the author did not observe a great deal of 'exploration' of the walls as horizontal surfaces. As the tunnels of the mesocosms were not flush with the floor of the boxes, it may have made it less likely for *F. auricularia* to encounter them. The failure of the tube as a BTP is thus twofold. The behaviours (foraging and sheltering) of interest may have been occurring on both sides of the tube, and the *F. auricularia* in the mesocosms may not have been capable of free movement across the tube (due to an inability to locate it).

Some limitations of the RFID system also became apparent during the experiment. The directional readers and controller were designed for use with bees. The movement of tagged *F. auricularia* (possibly compounded by the tube) appears to have confounded the ability of the readers to reliably determine the direction of movement. If an ideal situation for the RFID reader is imagined, a tagged insect should move directly and straightforwardly across the detecting area of the reader such that it is detected by one of the two antennas, then the other, in quick succession and within a 15-second cycle. Earwig 2 and Earwig 7 appear to be the only cases where this occurred, being the only individuals to be detected a single time, with a clear direction. Ignoring Earwig 9, the other detected *F. auricularia* appear to have made only a single transition through the tube, but slowly enough that the reader detected them in multiple 15 second cycles. This slower movement, potentially with some back-and-forth rather than a single trip through the tube, meant that often only a single antenna in the reader would detect a tag within a 15 second cycle, registering an "unknown" direction in the RFID system. However, even in cases where the RFID system had determined a direction of movement, examination of the data shows that errors were still being made. Earwig 11 provides a clear example, being detected only twice, but in both cases "arriving" (moving from the small box to the large box) with no other detection in between. The same occurred for Earwigs 1, 5, 8, and 9, indicating this was not an isolated incident.

Taken together, the observations and RFID data suggest very little movement between the two boxes of the mesocosms occurred. *Forficula auricularia* which did pass through the tube appear to have done so only once, and then remained in the large box, while 9 of 20 individuals never left the small box. As well as the limitations of the mesocosm design outlined above, this experiment was also completed on adult *F. auricularia* in March and April. At this time of year *F. auricularia* tend to be found sheltering in their burrows, and the adults are not known to feed. This may explain the overall lack of movement detected during the experiment, as well as the relatively high rate of deaths.

There are several changes the author would suggest in order to try and improve on the RFID mesocosm design for the study of *F. auricularia*. Figure 4.7 contains diagrams for several designs which could potentially generate useful behavioural data from tagged *F. auricularia*. Important points to consider are:

1. Experiments should be done during the growing season, when field populations of *F. auricularia* are naturally active. Fifth instar *F. auricularia* should be considered for experiments as well as adults.
2. RFID antennas or directional readers should not have an opaque cover that provides shade to the detection area. The iID®HIVE Entrance Reader AEB-03.C2D used in this experiment can be manufactured to fit this specification (Figure 4.8). Note that a transparent cover as part of the mesocosm will be required to keep tagged *F. auricularia* within the read range of the antenna/reader. The entire mesocosm should be brightly lit; only deliberately-placed shelters should provide shade/darkness.
3. Care should be taken to utilise the full width and height of the detection area of any RFID antennas/readers used. The BTP may need to be restricted in size to keep tagged *F. auricularia* within the read range of the antennas/readers, but this should be kept to a minimum.
4. The BTP/detection area should be flush with the floor of the rest of the mesocosm.
5. The area of the mesocosm on the side of a BTP designed to provide shelter should be as small as possible. Unlike the designs depicted in Figure 4.7, it may be ideal for this side of the BTP to consist entirely of the shelter with no superfluous space.

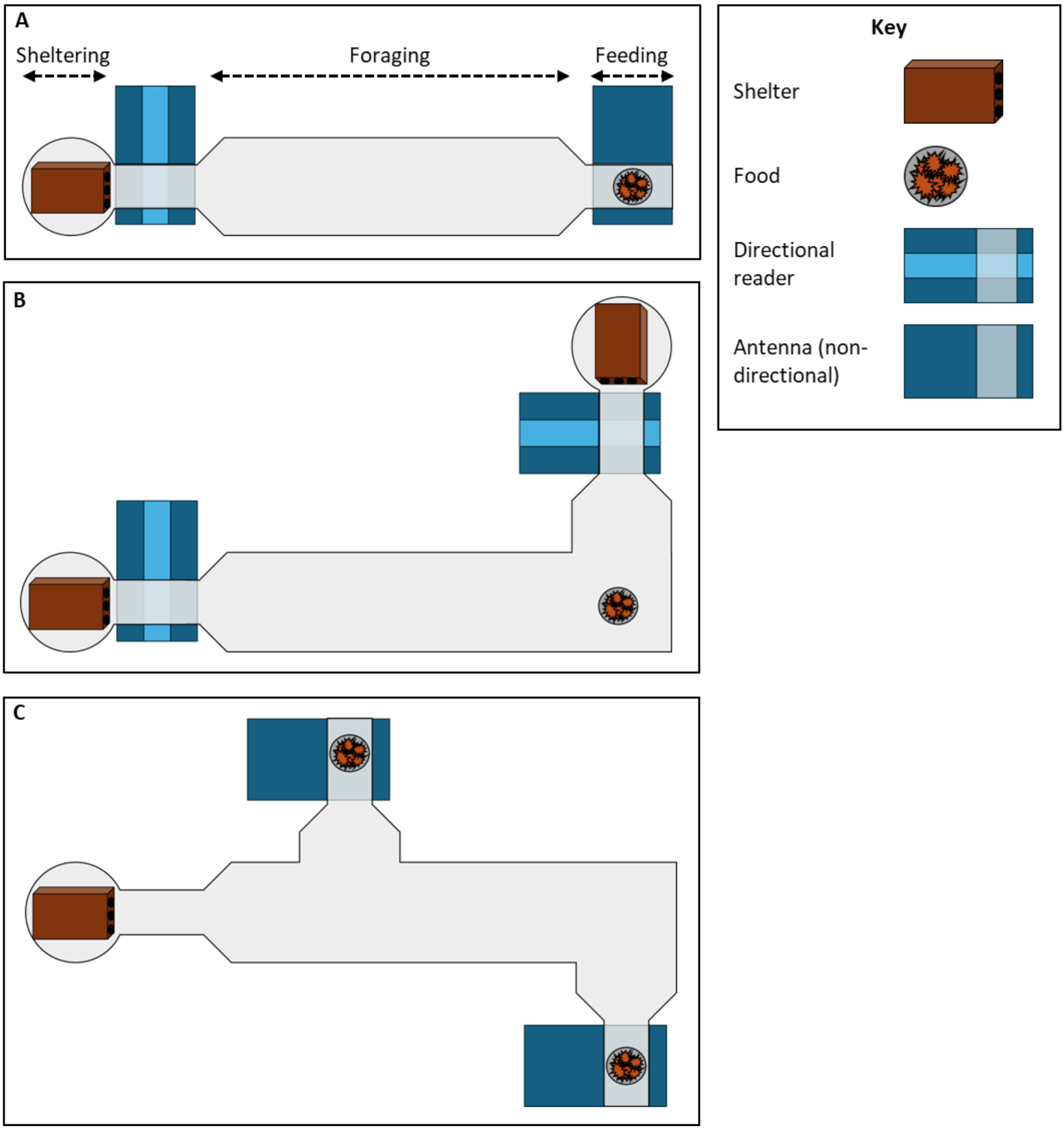

Figure 4.7. Potential designs for improved RFID-enabled mesocosms for the study of *F. auricularia* behaviour. A) A design using a directional reader and antenna to allow the study of sheltering, foraging, and feeding behaviour. B) A design which could be used to test if *F. auricularia* move to occupy shelters closer to food sources. C) A design which could be used with variable *F. auricularia* population densities to test if *F. auricularia* monopolise food sources. Not to scale.

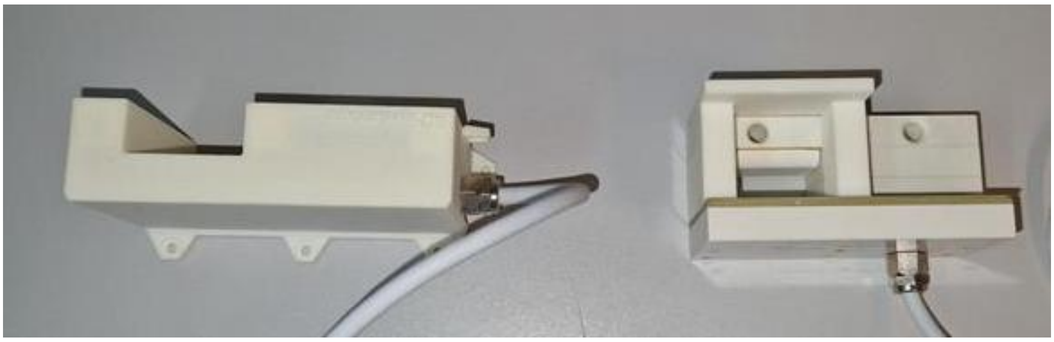

Figure 4.8. Two examples of iID®HIVE Entrance Reader AEB-03.C2D manufactured by Microsensys GmbH, Erfurt, Germany. On the left is an open-top reader, which does not have an inbuilt vertical constraint on the detection area. This design was not available during the mesocosm testing carried out in this study. On the right is the typical design, as used in this study. A vertical restraint on the detection area is present to prevent tagged insects from leaving the read range of the antennas while passing over the detection area. This design is built for integration with *Apis mellifera* hives.

While these alterations do not guarantee good data, they may assist in inducing clear and directed motion through the BTP, thus enhancing the ability of directional readers to correctly determine the direction of motion. They should also make the mesocosm easier for *F. auricularia* to navigate and ensure *F. auricularia* are at a point in their lifecycle where diurnal-nocturnal rhythms of activity are more natural. If a system and mesocosm can be designed which operates satisfactorily, a particularly interesting line of enquiry would be the influence of population density on the foraging and feeding behaviour of *F. auricularia*.

4.5. Conclusions

In conclusion, thermoplastic glue appears to be the best overall choice of glue for attaching RFID tags to *F. auricularia*. Cyanoacrylates are probably not suitable for use on *F. auricularia* and appear to be toxic, although the specifics of handling and tagging may moderate the degree of mortality these glues induce in *F. auricularia*. The prototype RFID mesocosms were successfully used to generate RFID data from tagged *F. auricularia*, and helped identify several key considerations that should be made when designing an RFID-enabled mesocosm for use with *F. auricularia*.

5. General discussion

5.1. Introduction

This research has made several key findings regarding the interactions between *Forficula auricularia* (L.) and *Eriosoma lanigerum* (Hausmann; WAA) in apple (*Malus domestica*; Bork) orchards. The aims of this project were:

- To investigate the presence of *F. auricularia* and WAA in commercial apple orchards and identify orchard characteristics associated with either species. Surveying and molecular gut content analysis were utilised to investigate the importance of *F. auricularia* predation of WAA.
- To assess the impact of providing artificial shelters for *F. auricularia*, on the abundance of both *F. auricularia* and WAA.
- To test commonly used glues for their effectiveness in attaching tags to *F. auricularia,* and for their toxicity, to aid future research. This included designing an RFID-enabled mesocosm for the collection of behaviourally relevant data on *F. auricularia*.

The key findings from this project were:

- *Forficula auricularia* appeared to contribute to the control of WAA in the orchards studied.
- The degree of WAA suppression was weaker in organic orchards in the years studied.
- *Forficula auricularia* was associated with bare earth, but not with several food sources or orchard management type.
- *Forficula auricularia* abundance may be limited by the availability of shelter in apple orchards.
- Radio frequency identification tracking may be used in mesocosms to study the behaviour of *F. auricularia*, but further improvements to the methodology are required.
- Cyanoacrylate based glues were toxic to *F. auricularia* and need to be avoided in future studies.
- Thermoplastic glue was the most effective at retaining the tag on the insect without increasing mortality and is recommended for future work.

5.2. *Forficula auricularia* and *Eriosoma lanigerum*

Chapter 2 demonstrated that *F. auricularia* was a contributor to the control of WAA. This is in agreement with many other studies which have shown the efficacy of *F. auricularia* 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 *F. auricularia* and WAA. This is important given that the main concern with *F. auricularia* 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 *F. auricularia*. 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 *F. auricularia*. However, it may lead to an underestimation of the value of *F. auricularia*, 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 *F. auricularia* 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 *F. auricularia* 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 *F. auricularia*. These insecticides are also not directly harmful to *F. auricularia*, 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 *F. auricularia* effective at WAA control. This highlights that *F. auricularia*'s 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 *F. auricularia* control of WAA in this study comes from populations of *F. auricularia* which had not been experimentally manipulated to enhance contrasts. There was no removal or release of *F. auricularia* (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 *F. auricularia* and indicate that with the correct management (*e.g.* minimal harmful insecticide sprays and no tillage while *F. auricularia* is overwintering; Fountain & Harris, 2015), expensive augmentative releases to control WAA might not be necessary. That being said, the *F. auricularia* populations in the orchards were monitored using refuge trapping (see below).

The finding of Chapter 3 suggests that artificial shelters can lead to increased *F. auricularia* abundance. This supports the findings of Moerkens *et al.* (2009), Jana *et al.* (2021) and Bischoff (*pers. comm.*). The implications of this for *F. auricularia* 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 *F. auricularia* enhances their abundance in trees, then studies relying on refuge trapping will tend to overestimate *F. auricularia* abundance in apple orchards, particularly later in the season. This may also bias studies (such as our own) which use refuge trapping to investigate *F. auricularia* and WAA interactions towards overestimating the effect of *F. auricularia* populations on WAA. In orchards without artificial shelters, *F. auricularia* 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 *F. auricularia*.

In Chapter 2 the rate of *F. auricularia* 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 *F. auricularia* immediately following predation. From this point onwards the probability of detecting WAA DNA will exponentially decay (Greenstone *et al.*, 2007). Because *F. auricularia* 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 *F. auricularia* immediately onto ice. When placed onto ice, *F. auricularia* 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 *F. auricularia* 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 *F. auricularia*'s digestion process (Cossins, 2012; Schulte, 2015). There was also the potential for the dissection procedure to contribute to low detection; 1) *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* 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 *F. auricularia*, 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 *F. auricularia*. It is worth noting that across 2022 and 2023, 944 samples, or 1,237 *F. auricularia* individuals, were processed. By comparison, Orpet *et al.* (2019a) sampled 315 *F. auricularia* 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 *F. auricularia* 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 (Chapter 2) 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.

5.3. *Forficula auricularia* distribution

Chapter 2 of this study was unable to identify many factors strongly linked to the presence of *F. auricularia* in orchard trees. Previous research has often found *F. auricularia* populations are highly variable and difficult to predict (Phillips, 1981; Burnip *et al.*, 2002; Gobin *et al.*, 2006, 2008; Moerkens *et al.*, 2009). It seems likely that given the temperature-dependent nature of *F. auricularia* development, this variability will become more extreme with climate change. Although some previous researchers have found a high degree of within-orchard variation in *F. auricularia* 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 *F. auricularia* caught in the refuge traps across all three surveys. The two other orchards owned by the same grower had 0 and 15 *F. auricularia*.

Forficula auricularia was 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 *F. auricularia* (other generalist predators), again cancelling out the reduced insecticide pressure. This is beneficial for growers, as it implies that all growers can benefit from *F. auricularia* as a natural enemy of WAA and other pests.

There were no strong correlations between *F. auricularia* 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 *F. auricularia* (Crumb, Bonn & Eide, 1941; Lamb & Wellington, 1975; Phillips, 1981). It seems unlikely that *F. auricularia* 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 *F. auricularia*. This may mean that, in apple orchards, factors besides food availability are more important in dictating the presence and abundance of *F. auricularia*.

This study did find a significant positive effect of a high proportion of bare earth in the row bed on *F. auricularia* presence. This was slightly unexpected, as flowering plants or moss cover should act as alternative food sources for *F. auricularia*. 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 *F. auricularia* is 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 *F. auricularia* eggs and nymphs (Atwell, 1927; Lamb, 1974; Phillips, 1981). Previous research has shown the timing of *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* overwinter outside orchards in Mediterranean citrus orchards (Romeu-Dalmau, Espadaler & Piñol, 2016). This would imply a seasonal migration of *F. auricularia* into and out of orchards each year, something which has not been observed. Other studies have shown that *F. auricularia* 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 *F. auricularia* in tree fruit orchards are influenced by the surrounding landscape. Traditionally, it has been thought that *F. auricularia* has poor dispersal under its own power (Crumb, Bonn & Eide, 1941). Part of this is that flight has been largely dismissed as an important factor in *F. auricularia* dispersal. However, it seems clear that under certain (uncharacterised) conditions, *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* has 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 *F. auricularia* into the orchards from surrounding areas. There is a lack of information on the status of *F. auricularia* 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 *F. auricularia* (Kocarek, 1998; Pavón-Gozalo *et al.*, 2011; Hill *et al.*, 2019). It may be that an understanding of *F. auricularia* population dynamics within apple orchards is incomplete without an understanding of populations in the surrounding environment.

Subspecies of *F. auricularia* 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 *F. auricularia* may differ in other important aspects of their biology (Moerkens *et al.*, 2010, 2012). It may be important to begin contextualising the results of *F. auricularia* 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 *F. auricularia* in apple orchards (Moerkens *et al.*, 2009; Jana *et al.*, 2021; Bischoff, *pers. comm.*). As discussed in Chapter 2, the addition of artificial shelters cannot lead to increased reproduction within the year of introduction, due to the length of the *F. auricularia* lifecycle. Artificial shelters may either reduce mortality, leading to a true increase in *F. auricularia* abundance, or concentrate *F. auricularia* 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 *F. auricularia* abundance in the surrounding area, as *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* populations (see above), then they may lead to a long-term decline in *F. auricularia* 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 *F. auricularia* was a reduction in predation by birds. However, Peusens *et al.* (2009) found no clear effect of bird exclusion on *F. auricularia*, 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 *F. auricularia* abundance inside of netted blocks. Older literature has mentioned starlings (*Sturnus vulgaris*; L.) as a potentially important predator of *F. auricularia*, 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 *F. auricularia* abundance. The role of predation in *F. auricularia* 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 *F. auricularia* derives 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 *F. auricularia* has 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 *F. auricularia* have begun to occupy tree canopies and have dispersed from their family units is unknown. If conspecifics did pose a significant risk to *F. auricularia* 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 *F. auricularia*.

5.4. Radio frequency identification

Given the many unknowns about *F. auricularia* 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 *F. auricularia* 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 *F. auricularia* adult body mass; Pope *et al.*, 2015; own data). Artificial shelters with RFID readers at the entrance/exit might be capable of repeatedly detecting *F. auricularia* 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 *F. auricularia* in the field prohibitively expensive, but this has not been explored. Compounding this is the difficulty of attaching tags to *F. auricularia*; they appear naturally suited to removing tags, as was found in Chapter 4.

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 *F. auricularia* 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 *F. auricularia* individuals forage multiple times in a night?
- Do *F. auricularia* 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 *F. auricularia* learn to navigate their immediate surroundings with greater speed over time?

Another interesting area to explore is the social dynamics of *F. auricularia* after the brood-tending stage. Pro-social behaviour has been reported while *F. auricularia* 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 *F. auricularia* 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.

Chapter 4 provided some of the first information on the feasibility of tagging *F. auricularia*, 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 *F. auricularia*, 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 *F. auricularia*, 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 *F. auricularia* 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 *F. auricularia*. 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 *F. auricularia* into without harm, but a slightly softer putty may be a better method of immobilising *F. auricularia* than bee marking cages.

As stated at the start of this section, the automated tracking of *F. auricularia* 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 *F. auricularia*. 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.

5.5. Grower recommendations

- Provide artificial shelters for *F. auricularia*
- Ensure there is bare ground in apple orchards or nearby for *F. auricularia* to nest
- Avoid tilling from November to May if possible
- Try to avoid spraying with insecticides harmful to *F. auricularia*, particularly in May, June, and July. Harmful insecticides include spinosad, indoxacarb, and deltamethrin
- Spirotetramat is appropriate for use with *F. auricularia*, and may enhance the benefits of having *F. auricularia* present
- *Aphelinus mali* and *F. auricularia* are compatible and both are desirable for WAA control
- If augmentative releases of *F. auricularia* are attempted, ensure these are carried out for multiple years
- Do not attempt to use sticky banding around apple tree trunks to control WAA
- If WAA infestation has become well developed during a growing season, *F. auricularia* will not be sufficient for control, but may help prevent resurgence in future years
- Alternative sources of food, such as wildflowers, may not benefit *F. auricularia* specifically, but may be advantageous for other beneficials
- If WAA does not appear to be a serious issue in an orchard, this does not mean that *F. auricularia* are of no benefit; they may be preventing colonisation

5.6. Conclusions

Overall, there is a great deal that is still unknown about *F. auricularia* 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 *F. auricularia* populations. There was evidence for an effect of *F. auricularia* on WAA populations in the orchards studied, without an augmentative release of *F. auricularia*. This effect appeared to be mediated by management practices, with more effective control of WAA by *F. auricularia* in conventionally compared to organically managed orchards. Radio frequency identification may not be an ideal for the remote monitoring of *F. auricularia* in the field in its current state, but it could be made easily applicable in mesocosm studies.

To the author's knowledge, the following statements concerning the contributions of this project to science are true:

- This study is the first to suggest *F. auricularia* may be more beneficial in conventionally-managed orchards rather than organic orchards
- It is one of only two studies to suggest bare earth may be beneficial to *F. auricularia*, and the first to attribute this to a real benefit rather than sampling bias
- This study is the first to test if the presence of lower plants is associated with *F. auricularia* presence
- This study represents the largest molecular gut content analysis carried out on *F. auricularia* (in terms of individuals sampled)
- This study is the third-largest investigation of *F. auricularia* and WAA interactions in terms of orchards sampled

- This study has shown that more work is required to design primers specific to WAA
- This study is one of only two studies directly comparing areas of apple orchards with *F. auricularia* artificial shelters provided to areas without shelters provided, and the first to test for an impact of this on prey abundance in apple orchards
- This study is the first to test glues for their effectiveness for tagging *F. auricularia*, and the first to test glues for their toxicity to *F. auricularia*
- This study is the first to collect data from RFID-tagged *F. auricularia*

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APPENDICES

A-1. The presence of *Forficula auricularia* and *Eriosoma lanigerum* in orchards in Kent

Table A-1. 2022 Survey Data

Please refer to attached file "Table_A-1_2022_Survey_Data.xlsx" for information on the orchard locations, orchard ages, agronomy information, aphid colony count data, earwig count data, and other scoring metrics for the 2022 survey work.

Table A-2. 2022 Gut Content Data

Please refer to attached file "Table_A-2_2022_Gut_Content_Data.xlsx" for information on the orchards sampled, dates of earwig collection, dates of earwig gut DNA extractions, and PCR results for the 2022 gut content analysis.

Table A-3. 2023 Survey Data

Please refer to attached file "Table_A-3_2023_Survey_Data.xlsx" for information on the orchard locations, orchard ages, agronomy information, aphid colony count data, earwig count data, and other scoring metrics for the 2022 survey work.

Table A-4. 2023 Gut Content Data

Please refer to attached file "Table_A-4_2023_Gut_Content_Data.xlsx" for information on the orchards sampled, growers sampled, dates of earwig collection, dates of earwig gut DNA extractions, and PCR results for the 2023 gut content analysis.

Table A-5. 2023 Pitfall Trapping Data

Please refer to attached file "Table_A-5_2023_Pitfall_Trapping_Data.xlsx" for information on the orchards sampled, the dates pitfall traps were set up, and the number of earwigs caught in each trap.

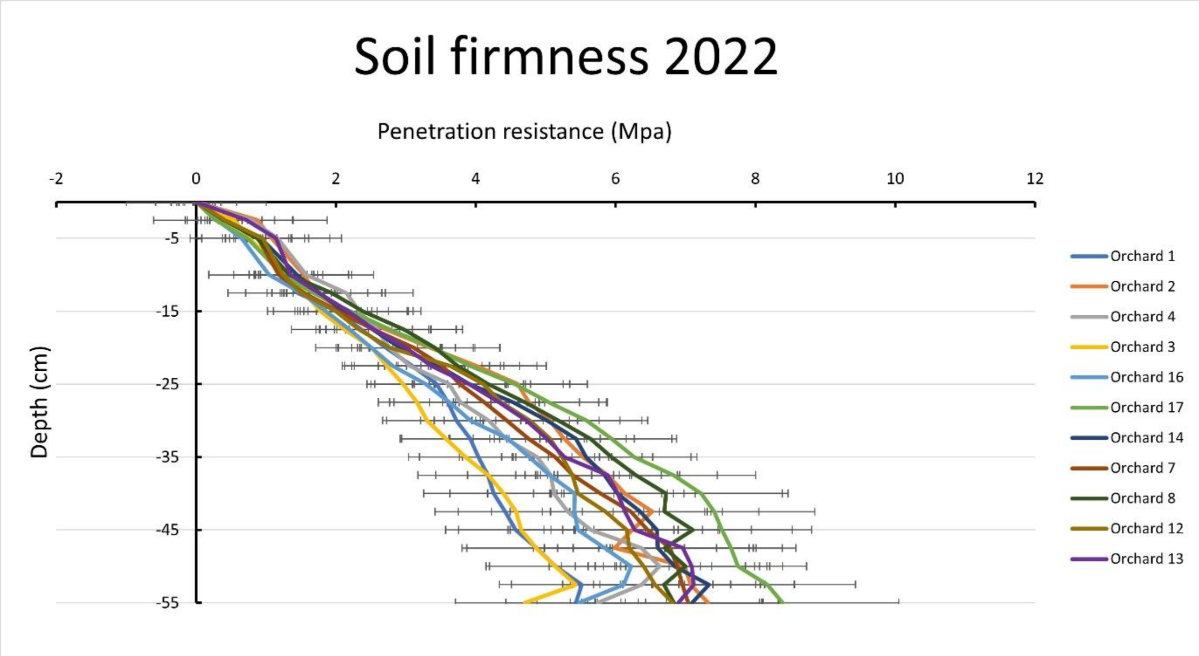

Figure A-1. Mean soil firmness measurements (MPa) taken from sampled orchards in the 2022 growing season across different depths ranging from 0 to 55 cm. Values have been corrected for moisture content and zeroed. Error bars represent standard deviation of the mean.

A-2. Impact of artificial shelters on the numbers of *Forficula auricularia* and *Eriosoma lanigerum* in an experimental apple orchard

Table A-6. Insecticide History

Please refer to attached file “Table_A-6_Insecticide_History.xlsx” for information on the insecticide treatment applications to blocks prior to this study. Note that records were missing for the years 2012, 2013, and 2014.

A-3. Radio frequency identification mesocosm designs for the study of *Forficula auricularia* behaviour

Video A-1. *Forficula auricularia* tag scraping during RFID experiments

Please refer to file “Video_A-1_ Forficula_auricularia_tag_scraping.mp4” to watch the following video. You can also access the video online using the following link: https://photos.app.goo.gl/R3FB2LBjK24GvpA86

Table A-7. Mesocosm Observations

Please refer to attached file “Table_A-6_Insecticide_History.xlsx” for information on the numbers of earwigs observed in the large box, the small box, the number of tags detached, dead earwigs, and earwigs introduced to the mesocosms.