

Insights into the behaviours of *Scolypopa australis* (Hemiptera: Ricaniidae)



Photo credit: Whyte (2011b)

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Photo credit: Yates (2022)



ABSTRACT

Scolypopa australis, commonly referred to as passionvine hopper (PVH), is a major pest impacting New Zealand's kiwifruit industry. Recent research on this insect has predominantly concentrated on innovating new management techniques, particularly the development of vibrational mating disturbance. This thesis delves into various facets of PVH behaviour, shedding light on their implications for future research in this domain.

Initially, I investigated the circadian rhythms of PVH vibrational calling behaviour, through laser vibrometry. In this experiment, I examined the likelihood of adult PVH engaging in calling behaviour at different times of day. While my observations indicated an increase in calling behaviour during darker hours, more comprehensive investigations are needed to confirm this pattern.

My second experiment sought to ascertain whether PVH exhibited protandry, a phenomenon common in species with similar characteristics to PVH. However, I discerned no significant differences in the emergence timings of adult males and females across the two seasons.

Lastly, I explored PVH's preference hierarchies regarding three plant species: māhoe, tomato, and blackberry. This investigation unearthed variations in preferences among the plant options, coupled with differences in preference behaviour between demographics, including nymphs, day-old adults, two-week-old adult males, and two-week-old adult females. While the exact drivers behind these distinctions warrant deeper investigation, it appears plausible that the resemblances I observed between nymph and two-week-old adult female preferences stem from ovipositing females seeking conducive sites to nurture their offspring's development. Furthermore, this experiment unveiled a significant aversion to tomato across all demographics. This revelation opens avenues for employing tomato in intercropping strategies, potentially serving as an additional deterrent for PVH in kiwifruit orchards.



Overall, this work provides some basic information that is much needed to further our understanding of PVH for the management of this pest species and highlights many areas where more information is needed.

CHAPTER 1: INTRODUCTION

COMMUNICATION

In biology, communication refers to the transmission of signals from one organism to manipulate the behaviour of another, with the sender ultimately benefiting from this exchange (Krebs & Dawkins, 1984; Searcy & Nowicki, 2005; Davies et al., 2012). Otte (1974) defined signals as "...behavioural, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms". These characteristics are selectively advantageous for communication and exclude instances where a sender transmits information that is not beneficial to them when received by another organism, such as kairomones – semiochemicals emitted by an organism facilitate interactions between different species, benefiting the recipient while causing harm to the emitter (Brown et al., 1970). Further, communication does not necessarily benefit the recipient of a signal, such as in cases of deception (Otte, 1974; Searcy & Nowicki, 2005).

Krebs and Dawkins (1984) posited that just as animals can leverage objects in their environment to their benefit, such as an otter using a stone to crack open an oyster, they are similarly inclined to exploit other animals for their advantage. This dynamic can lead to an evolutionary tension where a species must balance maximizing individual fitness (defined as the number of reproductive offspring it produces) through deception, while also developing resistance to deception from conspecifics. The reliability of a signal for the recipient can be determined by assessing the correlation between the signal and the attribute it represents (Searcy & Nowicki, 2005).

This is well exemplified in anurans (frogs and toads), as described by Searcy & Nowicki (2005). In these species, males with larger body sizes have several advantages, for example, increased access to mates and the ability to deter competition from other males. Notably, there tends to be a strong correlation between body size and the fundamental frequency of male croaking. As a result, croaking has evolved as a reliable signal of body size among conspecifics (a.k.a. an 'icon'; Maynard Smith & Harper, 2003). This signal is considered "honest on average", indicating that recipients are more likely to interpret it as honest due to its high probability of accurately representing body size (Johnstone & Grafen, 1993).



Nevertheless, male frogs are also subjected to the evolutionary pressure of generating attractive vocalizations without expending physical resources on having a larger physical size. They may achieve this by modifying characteristics such as vocal cord mass. As a result, they have the potential to develop deceptive signals that entice females without offering the advantage of a larger mate. This dynamic creates an evolutionary arms race between the 'manipulator' and the 'mind-reader' in terms of the signal's reliability (Krebs & Dawkins, 1984).

However, in reality, communication systems are not always characterized by such antagonism. While Maynard Smith and Harper (2003) agreed that conflicts of interest between signallers and receivers often result in such dynamics, they also posited that evolutionary pressure will eventually result in the 'perfection' of both manipulation and mind-reading wherein both parties, on average, derive benefits from the interaction.

The ubiquity of communication systems throughout the living world demonstrates their utility as a survival tool. The development of communication provides several adaptive advantages, especially when it comes to coordinating behaviour. The ability for an individual to share information and influence the behaviour of other organisms in its environment allows for the existence of more complex tasks that reap greater fitness benefits at a population-level, such as sexual reproduction, resource gathering, and defence (Gärdenfors, 2004).

CIRCADIAN RHYTHMS

Another adaptation that facilitates coordination of behaviour is circadian rhythms. Circadian rhythms are internal processes that regulate the timing of various physiological and behavioural functions in living organisms (Nation, 2022a). They follow a roughly 24-hour cycle and are influenced by environmental cues, most often the light-dark cycle (Nation, 2022a). These rhythms play a crucial role in coordinating daily activities, such as sleep-wake cycles, hormone production, metabolism, and other biological processes (Nation, 2022a). Coordinating behaviour with regular intervals is crucial for the overall functioning of a population. For example, within-species synchronization of mating activity is particularly important for reproductive success (Sakai & Ishida, 2001).

Consequently, different properties of communication may be adapted to follow circadian rhythms. Ethological studies tracking communicative behaviour in organisms over daily cycles can reveal important information as to the timing of different behaviours. To illustrate these adaptive advantages, consider that mating-related communication in many species occurs at specific times of day. For example, some moths release pheromones at specific times to attract mates (Levi-Zada & Byers, 2021). This temporal coordination allows individuals to maximize the chances of successful mating by ensuring that their signals are effectively received and responded to by potential mates.

BIOTREMOLOGY

Biotremology is *the study of vibrational communication behaviour*, i.e., the transfer and perception of information utilizing substrate-borne vibrations (Mortimer, 2017; Hill et al., 2019). Previously considered to be a part of bioacoustics (the study of sound), biotremology as a discipline was only defined in 2014, although there is considerable overlap between these subjects. Both involve the production of vibrations transmitted across a medium which are used as signals for communication, and both involve signals that are received by mechano-receptors (Hill et al., 2019). The main distinction between biotremology and bioacoustics posed by Hill et al. (2019) is that acoustic communication travels through gasses or liquids, which are “relatively homogenous” media that supposedly do not significantly distort the signal’s waveform. Conversely, vibrational communication traverses solid media which is more heterogenous. However, I believe this claim is somewhat inaccurate. Both gases and liquids can be heterogeneous; changes in temperature, density, humidity, and turbulence alter the way in which sounds propagate through gasses and liquids, causing distortion (Hawkins, 1986; Eliopoulos, 2005). The principal reason biotremology has arisen as a distinct subject is to combat perceptual bias. The primary form of communication between humans is vocal (Adler et al., 2016), and because of this we are naturally biased towards studying auditory communication (Caves et al., 2019). Biotremology puts an important emphasis on considering sensory experiences other than those we, as researchers are inherently familiar with.

Vibrational communication is observed in a wide range of animals (e.g., mammals such as elephants and mole rats (Mason & Wenger, 2019), amphibians (Narins, 2019), chameleons

(Barnett et al., 1999), and fiddler crabs (Aicher & Tautz, 1990)). However, the majority of examples of vibrational communication have been found in insects. Ninety-two percent of insects that belong to families that communicate through mechanical disturbances use vibrational communication, and 71% use this medium exclusively (Corcroft & Rodríguez, 2005). In total, over 195,000 described insect species make use of vibrational communication (Cocroft & Rodríguez, 2005). In particular, the order Hemiptera has been at the centre of many biotremology studies (Hill et al., 2019), due in large part to many hemipterans, such as aphids, scale insects, and mealybugs, being major crop pests of economic importance (Omkar, 2021).

Vibrational communication used in courtship and mating contexts has been especially well studied in insects. Mating generally follows a courtship sequence which involves different types of communication at different stages of the sequence (Endler, 2019). Vibrational communication can be used at any stage, provided that the communication is not long-range, as signal quality is affected by noise and distortions the further it travels (Endler, 2019). Michelsen et al. (1982) found that vibrational signals from several hemipterans were able to traverse through many plants – both woody and herbaceous – for several metres without decaying. However, distortions were caused by signals reflecting off the edges of the plant.

Hill et al. (2019) used *Aphrodes makarovi* (Hemiptera: Cicadellidae) to exemplify how vibrational communication is used during different stages of mating. Initially, males alert their presence to potential mates using advertisement calls, which are spontaneous vibrational signals emitted by solitary insects (Avosani et al., 2020). If this gains the attention of a receptive female, she will call back to indicate her location. The male and female then duet back and forth until they locate each other. This behaviour also informs the female of mate quality, as male calls attract the attention of both predators and other competitive males. Males that invest more in competitive behaviour, such as masking the calls of other males, facilitate quicker location of the female, resulting in higher mating success (Hill et al., 2019). Due to its prevalent use in reproduction, the study of biotremology has important ramifications for the control of insects that are considered pests of crops of economic importance.

BIOTREMOLGY AND INSECT PEST CONTROL

Around 150,000 insect species solely rely on vibrational sexual communication. These include planthoppers (Hemiptera: Fulgoromorpha) and leafhoppers (Hemiptera: Cicadellidae) (Claridge, 1985; Cocroft & Rodríguez, 2005), many of which are agricultural pests.

Pesticides have played a vital role in improving the quality and quantity of crop yields, and therefore food security, for thousands of years (Panagiotakopulu et al., 1995; Sharma et al., 2019). However, with the rapid expansion of agriculture and advancements in chemical engineering since the industrial revolution, the volume and diversity of pesticides being utilized has increased to ~2 million tonnes being used annually (Sharma et al., 2019). This has resulted in a wide array of unintended damages. Pesticides are able to disperse into the environment and enter the food chain via surface and subsurface run-off, spray drift, dust, and vapour transport (Waite et al., 2005; Reichenberger et al., 2007; Ellis et al., 2010; Gupta & Gupta, 2020). Consequently, these chemicals have a tendency to accumulate in food chains, leading to the bioaccumulation of toxins (Gupta & Gupta, 2020). For instance, the use of organochlorines in insecticides has been linked to the presence of carcinogenic compounds in humans (Stellman et al., 2000; Sharma et al., 2014). Insecticides are also a major contributor to global declines in insect biodiversity (Sánchez-Bayo & Wyckhuys, 2019).

In response to mounting evidence of the dangers of chemical pesticides to human, environmental, and agricultural health (Pimentel & Burgess, 2016), regulatory agencies worldwide are working to implement safer, integrated pest management techniques. For example, policy initiatives put in place by the European Green Deal promote the use of low-risk and non-chemical pest control and seek to cut the usage of chemical pesticides in half by 2030 (European Commission, 2020). As such, there is growing market demand for alternative pest control options.

Signals involved in mating need to be species-specific and highly attractive to ensure reproductive success. Because of this, interfering with mating-related communication can be an effective method of controlling insect pests, with the added benefit of decreasing dangers to non-target species (Polajnar et al., 2015). For example, sex pheromones have been used to disrupt mating by confusing the target species through overexposure of the chemical sensory system or leading them on false trails (e.g., Evenden et al., 1999). However, the artificial synthesis of these pheromones can be a tedious and costly process as they need to be

extremely accurate so as to avoid attracting the wrong species, and as such may be made from a plethora of diverse compounds (Howse et al., 1998; Evenden et al., 1999; Ioriatti & Lucchi, 2016).

Vibrational communication is another form of sexual communication that can be manipulated for pest control through the use of vibrational mating disruption (VMD) (Mazzoni et al., 2009b). As previously noted, when a male insect detects a conspecific male's mating calls, he may choose to competitively interfere with that signal by masking it with disruptive noise. Humans can similarly interfere with insect mating by exposing pests to mechanical vibrations that block sexual communication.

Saxena and Kumar (1980) were the first to attempt the use of VMD. They exposed mating pairs of *Amrasca devastans* (Hemiptera: Cicadellidae) to sounds generated in the air by “various devices (sic),” including running motors and a reed organ. While this did disrupt mating, the volume needed for the airborne sound to vibrate the substrate the insects were on was too loud, unpleasant, and/or impractical to be used in any real-world setting. Since then, technological advances have resulted in several instances of VMD being used successfully to control insect pests, particularly in the last decade. For example, *Scaphoideus titanus* (Hemiptera: Cicadellidae) is a disease-spreading vineyard pest that uses vibrations to recognize and locate potential mates (Papura et al., 2012; Polajnar et al., 2016). Their courtship behaviour, as described by Mazzoni et al. (2009c) and Polajnar et al. (2014), follows a similar sequence to *A. makarovi*, including the phenomenon of sexual interference from rival males. When rival males detect a female pulse response to male advertisement calls, they emit disruptive noise which impedes the male's ability to locate the female. Indeed, males will stop searching entirely if the female's call has been compromised. In a follow-up study, Mazzoni et al. (2009b) found that the playback of digitally synthesised disruptive noise could be used to significantly reduce the number of copulations.



Figure 1: set-up of vibrational transducers in a vineyard from Mazzoni et al. (2019b)

These findings were used by Mazzoni et al. (2019b) to develop a VMD system using mini-shakers attached to trellis poles that transmitted disruptive noise along its wires (Figure 1). They began testing this set-up in 2017 in an organic vineyard in San Michele all'Adige, Italy. After two years of observation *S. titanus* numbers had decreased by ~50% in the treated vineyard compared with the control, and *Empoasca vitis* nymphs, another grapevine pest, had decreased by ~25%. Additionally, they discovered no impacts on other non-target species (Mazzoni et al., 2019a). More recent work has also found that that exposure to VMD significantly reduces oviposition, and increases flight activity in *S. titanus* (Zaffaroni-Caorsi et al., 2022).

This success inspired researchers to pursue VMD for *Homalodisca vitripennis* (Hemiptera: Cicadellidae), a vector of the bacterium *Xylella fastidiosa*, which is the causal agent for Pierce's disease in grapes, and citrus variegated chlorosis in citrus (Gordon & Krugner, 2019). Their basic courtship behaviour was outlined by Nieri et al. (2017), who found that, like other leafhoppers, *H. vitripennis* primarily use substrate-borne vibrations during mating and exhibit conspecific rivalry between males. Rival males "catfish" each other by imitating female calling signals when they are exposed to male-female duets. Subsequent laboratory research evaluated *H. vitripennis*' behavioural reactions to various playbacks and discovered that white noise and female signals significantly suppressed mating (Gordon et al., 2017; Mazzoni et al., 2017). It was also demonstrated that vibrational playback could take advantage of female-female competition. When two females are present on a plant, they will assess each other's quality by duetting until the weaker one gives up. Females compete in signalling competitions with the playback to establish dominance over what they perceive to

be a weaker signal. However, because the playback is set to play continuously, she exhausts herself and is unable to attract males (Gordon et al., 2017). Finally, in a field experiment similar to that by Mazzone et al. (2019b), vibrational transducers broadcasting modified female signals connected to a grapevine trellis resulted in a reduction of mating success from 20% to 3.2% (Gordon & Krugner, 2019).

PHENOLOGY

Phenology, the study of timing in biological life cycles, helps in understanding the role of external cues in coordinating behaviour within populations (Schwartz, 2013). Insects employ phenological patterns, with many species aligning their life stages – eggs, larva, pupae, and adults – with specific environmental cues such as temperature, day length, or availability of host plants (Mjaaseth et al., 2005; Nietschke et al., 2007; Salis et al., 2017).

Sexual bimaturism, another phenological phenomenon, describes situations where adult emergence times differ between males and females (Singer, 1982; Morbey, 2013; Teder et al., 2021). A meta-analysis of 192 species of insects found that protandry, where males emerge before females, is prevalent in 65% of surveyed insects, and is commonly associated with species in which females take longer to develop (Teder et al., 2021). However, the direction and intensity of sexual bimaturism can shift dramatically between generations due to factors like larval development time plasticity, with adverse early-life conditions affecting females more than males (Teder & Kaasik, 2023). Sexually dimorphic development times in insects often arise from sexual size dimorphism, with females usually having larger adult body mass (Teder & Tammaru, 2005; Teder, 2013; Esperk et al., 2007; Honěk, 1993). Further, there is a strong correlation between female body mass and fecundity (Honěk, 1993). In the Auchenorrhyncha suborder, females are commonly larger than males, and instances of protandry are prevalent, with the degree of protandry often influenced by temperature during nymphal development (Constant, 2005; Constant, 2006a; Constant, 2006b; Rahman et al., 2011; Constant, 2018; Wang et al., 2020; Razak et al., 2023; Chuche & Thiéry, 2012; Hou et al., 2015; Xiao et al., 2023). Other predictors of protandry include environmental seasonality, and discrete non-overlapping generations, especially in species with greater female development time caused by their heightened sensitivity to adverse conditions (Morbey, 2013; Singer, 1982; Yamamura & Kiritani, 1998; Teder & Kaasik, 2023).

PLANT PREFERENCES AND FORAGING IN POLYPHAGOUS INSECTS

Polyphagous insects exhibit preferences for certain plants despite their broad diets, as they have evolved to specialize in consuming nutritionally optimal or easily accessible food sources (Jermy, 1985). However, these preferences are subject to various selection pressures and trade-offs. For instance, high-quality plants may be scarce or attractive to natural enemies, while common plants may be less nutritious. Additionally, parent-offspring conflict can arise when ovipositing adults have different dietary needs than their offspring (Scheirs & De Bruyn, 2002). These preferences reflect the evolutionary and environmental adaptations of polyphagous insects to optimize their nutrient intake and survival (Cunningham & West, 2001).

The preference hierarchies of polyphagous insects can be complex. The food preferences of polyphagous insects can be either innate or induced. Innate preferences are those that are present from birth and are determined by genetics, although they can be refined by experience. On the other hand, induced preferences are those that are learned or influenced by environmental cues. Experience during juvenile stages has been shown in many species to have strong impacts on the preferences of individual insects. Repeated consumption of a host plant often leads to a preference for that food source over others, a phenomenon known as an induced preference (Jermy et al., 1968; Jermy, 1985). For example, the moth *Spodoptera littoralis* exhibits innate preference hierarchies, with the exception that they always exhibit the strongest preference towards whatever species they were reared on as larvae (Thöming et al., 2013). An explanation for this is that insects in environments with unstable host assemblages must make a trade-off between optimal hosts and available hosts. The plant the insect was reared on is likely to still be present when that insect seeks hosts for its own offspring, so developmental plasticity and preference induction during larval stages allows the insect to avoid searching for optimal, yet rare, hosts.

Induced preference has also been observed in several hemipterans. For example, a study by Schweissing and Wilde (1979) on *Schizaphis graminum* found that the host species they were cultured on had impacts on their dietary preferences. The grain type the insect was reared on correlated to different preferences as adults. Interestingly, this did not always result in a preference for the grain they were reared on. Juvenile experience may also induce oviposition preferences in adult females. Adult *Diaphorina citri* exhibited a preference for

ovipositing on host plant species they were reared on, and this effect increased when reared on hosts that provided greater offspring fitness (Stockton et al., 2017).

PEST MANAGEMENT: INTERCROPPING

Intercropping, the practice of growing multiple crops together in the same field, can be used as a management strategy for insect pests by creating a diverse agroecosystem that promotes natural pest control (Smith & McSorley, 2000). This concept is based on the Resource Concentration Hypothesis, which suggests that diverse crop stands make it harder for pests to find their host plants, leading to lower pest populations and reduced damage (Finch & Collier, 2000; Smith & McSorley, 2000). Intercropping can attract beneficial insects that control pests while repelling or deterring pest insects (Tscharrntke et al., 2007; Letourneau & Bothwell, 2008). By way of illustration, intercropping with unsuitable hosts has been effective in reducing populations of the silverleaf whitefly, *Bermisia tabaci* (Hilje & Stansly, 2008; Zhao et al., 2013; Gold et al., 1989). Additionally, volatile organic compounds from certain plants can repel pests or hinder their ability to locate host plants (Carvalho et al., 2017; Togni et al., 2010). Intercropping provides multiple mechanisms for pest management and can contribute to sustainable agriculture practices.

STUDY SPECIES: PASSIONVINE HOPPERS (SCOLYPOPA AUSTRALIS)



Figure 2: Adult and nymphal passionvine hoppers (Scolytopa australis) aggregated on a plant stem (Whyte, 2011a)

Passionvine hoppers (PVH), *Scolytopa australis* (Walker, 1851) (Hemiptera: Ricaniidae), are a polyphagous, phloem-feeding insect introduced from Australia to New Zealand around 1878 (Hill & Steven, 1989). Passionvine hoppers undergo one generation per year, with significant overlap between developmental stages (Cumber, 1966; Larivière et al., 2010) (Figure 2). Nymphs primarily emerge from October to December, but in cooler southern areas nymphal emergences may be delayed until February (Cumber, 1966; Hill & Steven, 1989). Adults typically emerge from late December to April (Hill & Steven, 1989), with adult activity peaking from January to March (Cumber, 1966), although they may emerge earlier in warmer regions (Matheson, 1978). Over the winter, PVH populations persist only as diapausing eggs laid inside dead and living plant stems (Cumber, 1966; Matheson, 1978; Fletcher & Anderson, 1980; Gerard, 1989; Logan et al., 2017).

DISTRIBUTION

In Australia, PVH can be found throughout the East coast, and Tasmania (GBIF.org, 2 August 2023). In New Zealand, their range currently extends as far south as Christchurch, in the middle of the Canterbury region of the South Island, with a single observation as far south as Kurow, at the bottom of the Canterbury region (Figure 3). This range expansion is recent; data from GBIF.org (2 August 2023) shows that prior to around 2018, PVH could only be found in the North Island, and uppermost portions of the South Island (Figure 3).

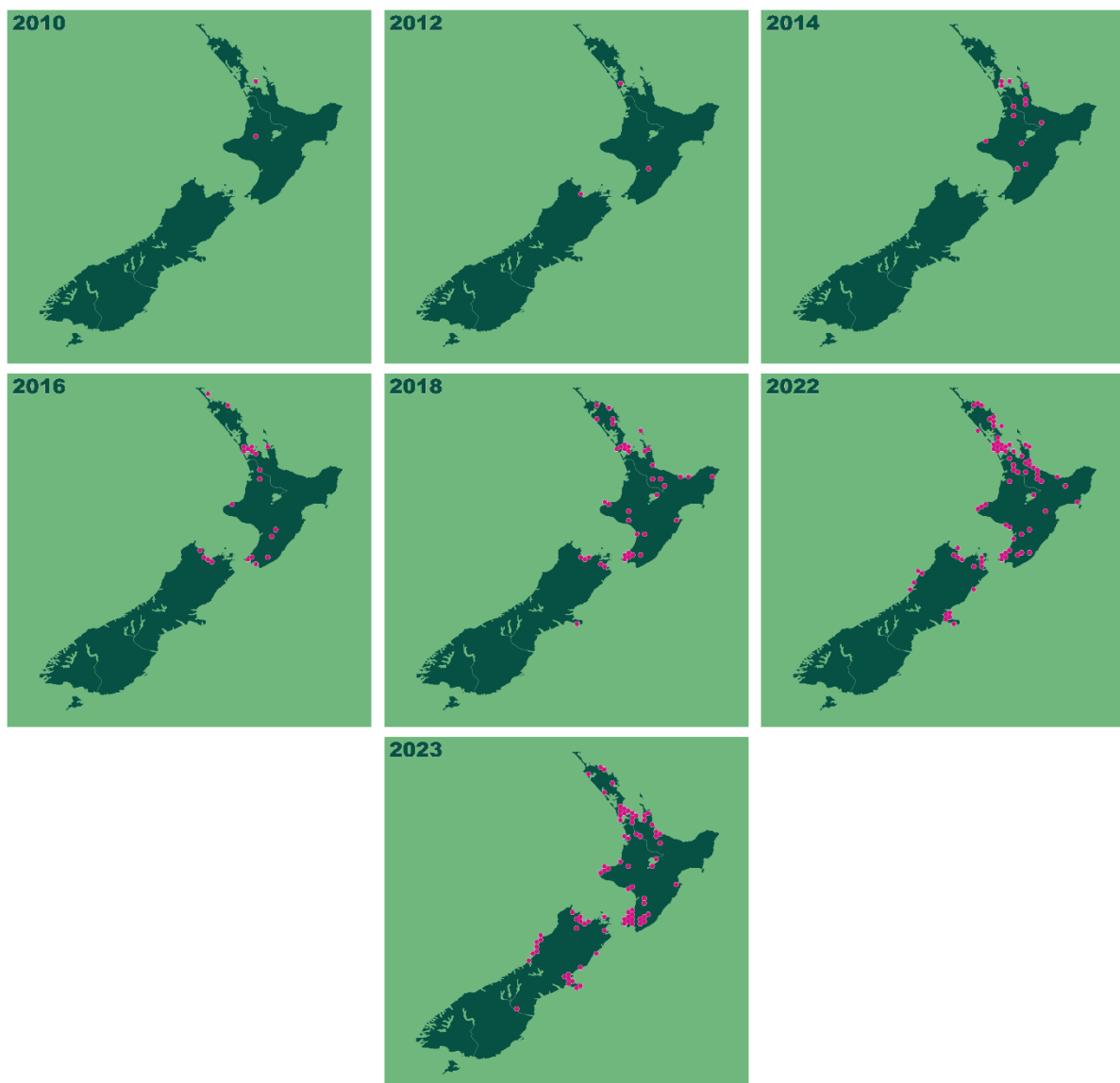


Figure 3: Passionvine hopper observations in New Zealand each year, from 2010 to 2023 (GBIF.org, 2 August 2023)

However, it should be noted that the majority of the reports of PVH in the GBIF dataset were from iNaturalist, a citizen science website launched in 2008, which relies on user access to a mobile phone or computer to contribute observations. Indeed, according to Lloyd

Stringer (pers. comm.), PVH could be found in Christchurch as early as 2013. Prior reporting on the range of PVH found that they were previously only widespread in areas below 500m in the North Island, and in the uppermost portions of the South Island (Cumber, 1966; Matheson, 1978). As no published reports on their range using newer data have been released since 1978, the range expansion of PVH further south could have potentially happened any time within the last 35 years. Matheson (1978) noted that there was a close correlation between Cumber's (1966) distribution maps and local temperatures. He found that PVH tended to be located in areas with an average July temperature isotherm of 8°C, an average maximum daily July temperature of 12°C, and a mean annual temperature isotherm of 12°C.

The expansion of PVH's range further south may be due to climate change, as this is known to affect the ranges of insect pests (Battisti & Larsson, 2015). Using data from NIWA's national climate database (CliFlo, 2023), I briefly investigated the mean and mean daily maximum air temperatures from 1966 to 2022, both annually and in July from Christchurch based weather stations using Microsoft Excel (Microsoft Corporation, 2018). I found that there were moderate to weak correlations between year and average annual temperatures ($R^2 = 0.362$), average July temperatures ($R^2 = 0.277$), and average daily maximum July temperatures ($R^2 = 0.365$). Further, average July temperatures have never reached 8°C. This means that this range expansion cannot fully explained by the trend Matheson (1976) noted. Further, Gerard (1985) found that PVH require an average annual temperature of 14-15°C to meet the required number of degree days to fully develop. However, Gerard (1985) also noted that PVH may still be able to persist in warm, sheltered sites, like urban heat islands, which are created by the warming effect of structures that absorb and retain heat in urban areas, such as pavement (Zhao et al., 2014).

ECONOMIC IMPACTS

In te reo Māori, the region of the Bay of Plenty is known as *Te Moana-a-Toi*, or, more fully as *Te Moana a Toi-te-Huatahi*. This translates as "*The Ocean of Toi of the First Fruits*" and is an apt name for the region. The Bay of Plenty is also known as "*The Kiwifruit Capital of the World*." In this area, PVH thrive in pockets of native bush, and spill-over into neighbouring orchards during the summer. Attempts to block invaders by clearing scrub bordering orchards

are ineffective, as PVH can disperse at least 70 m, if not further, in open areas (Tomkins et al., 2000).

Due to the nature of their feeding, PVH excrete large amounts of honeydew in the locations where they feed. On kiwifruit, this honeydew encourages the growth of sooty-mould fungus. A report from Zespri™ (Wilson & Barker, 2020) found that sooty-mould cost New Zealand's kiwifruit industry \$76.36 million in 2018/19. Although PVH are not the only insects contributing to sooty-mould growth in kiwifruit orchards (other organisms include cicadas, mealybugs, and soft scale insects), the fact that they lay eggs inside fruit stalks means they are protected against many pesticide sprays (Steven, 1990; Gaskin et al., 2012).

Passionvine hoppers also pose a risk to New Zealand's apiculture industry. Tutin is a phytotoxin produced by tutu (*Coriaria arborea*), a native shrub common throughout New Zealand. Honeydew produced by PVH feeding on *C. arborea* is consumed by honeybees. Subsequently, humans eating tutin-contaminated honey may experience vomiting, seizures, and even death (Beasley et al., 2018). Mitigating the risk of tutin contamination requires rigorous management by beekeepers, as outlined by the Ministry for Primary Industry's Food Standards (Ministry for Primary Industries, 2020).

Several studies have explored the role of natural enemies as potential biocontrol agents to manage PVH. Logan et al. (2020) investigated the egg parasitism of *S. australis*, highlighting the presence of egg parasitoids such as *Centrodora scolypopae* and *Ablerus* spp. These parasitoids exhibit varying distribution patterns across different regions and have been recognized as potential agents for controlling PVH populations; for example, *Ablerus* spp. are a direct egg parasitoid of PVH rather than a hyperparasitoid of *C. scolypopae*, as was initially assumed. Charles and Allan (2012) further elucidated the expansion of *C. scolypopae*'s range across New Zealand since its initial identification and the potential of entomopathogenic fungi as natural enemies of *S. australis* has also been explored by isolating highly pathogenic *Lecanicillium muscarium* from cadavers of PVH, showcasing the potential of this fungus to serve as a biocontrol agent (Marshall et al., 2003). The seasonal population dynamics of PVH and its interactions with natural enemies highlight the presence of various natural enemies, including predatory insects and spiders, contributing to the regulation of PVH populations (Gaskin et al., 2012). Collectively, these studies underscore the significance of natural enemies in influencing the population dynamics of PVH and suggest the potential for utilizing specific

parasitoids and entomopathogenic fungi as effective biocontrol strategies to manage this pest in agricultural settings.

DIETARY PREFERENCES

Logan et al. (2002) conducted a study focusing on the dietary and oviposition preferences of PVH. The first part of this study was a field survey conducted in the Bay of Plenty during October of 2001 and 2002. They observed that both adult and nymphal PVH can be found on a wide range of native and introduced plants. Aggregations of insects were notably observed on specific plant species such as pepper trees (*Piper excelsum*) and māhoe (*Melicytus ramiflorus*), indicating potential preferences for feeding and development sites. In this study, they also performed choice and no-choice tests on nymphs and adults. In the choice tests, first-instar nymphs and adult PVH were introduced to cages containing four different plant species, revealing their preferences for certain hosts over others. In choice tests, both first-instar nymphs and adult PVH exhibited distinct preferences among the available host plants. Nymphs were unevenly distributed among the plants, favouring *M. ramiflorus*, and blackberry (*Rubus* spp.) over *P. excelsum*. Similarly, adult PVH demonstrated a preference for *M. ramiflorus* over other options after both 7 and 32 days, and fewer adults were found on blackberry and honeysuckle (*Lonicera japonica*) than on *M. ramiflorus*. The number of egg-laying scars varied between plant species, with *P. excelsum* having fewer scars compared to *M. ramiflorus*, blackberry, and *L. japonica*. These choice experiments underscored the host preferences of different life stages of PVH and its implications for survival and reproduction.

In Logan et al.'s (2002) no-choice tests, nymphs and adults were separately placed in cages with single plant species, measuring survival rates, developmental stages, and egg-laying behaviours on specific host plants. Host plant selection significantly impacted both the longevity and fecundity of adult PVH, with the longest average longevity recorded on wineberry (*Aristotelia serrata*), fleabane (*Conyza* spp.), and *M. ramiflorus*. Furthermore, egg-laying behaviour differed among host plants, with *A. serrata* exhibiting the highest number of egg-laying scars. This experiment highlighted the interplay between host plant selection, adult lifespan, and reproductive success, contributing to a deeper understanding of the factors influencing PVH populations.

The information gleaned from the choice and no-choice experiments on host preferences of PVH can be valuable in designing intercropping strategies. By strategically selecting and arranging plant species based on the hopper's preferences, intercropping systems can be optimized to deter or attract these pests, contributing to more effective pest management and enhanced crop yields.

VIBRATIONAL COMMUNICATION

The use of vibrational communication in PVH was recently described by Sullivan et al. (2022). The vibrations of lone, unmated males and females were recorded, along with preliminary trials involving male-female pairs. In the single-sex trials, 29% of recorded males and 36% of recorded females produced at least one calling signal within 30 min. Analysis of these signals revealed a male calling signal (Appendix 1A) composed of pulses (a singular, homogenous sound parcel of finite duration that consists of a brief series of sine waves; Alexander, 1967) arranged in pulse trains (a sequence of pulses organised into temporally different groups; Avosani et al., 2020) increasing in amplitude, and two female calling signals (Appendix 1B-E) which differed in how pulse trains were dispersed. Additionally, the second female signal (Appendix 1D, E) somewhat resembled advertisement calls used by female *Philaneus spumarius* (Avosani et al., 2020). Like many other auchenorrhynchans, adult males began generating calls earlier than females and the signal structure of male calls varied considerably more, and lasted longer, than females (Mazzoni et al., 2009c; Nieri et al., 2017; Avosani et al., 2020). Since vibrational signalling is energetically costly, it is likely that females are using male calls to evaluate the quality of potential mates. During the male-female trials, no instances of duetting or mating were observed.

Nevertheless, Sullivan et al. (2022) made an interesting observation: calling activity showed an increase later in the day. This aligned with reports from colleagues in the field (David Logan, pers. comm.), who exclusively documented mating of PVH in the evening. It is worth noting that the recordings made by Sullivan et al. (2022) were conducted between 09:00 and 16:00, which potentially fell outside the appropriate timeframe for observing mating.

Based on this, the researchers put forth a hypothesis suggesting that calls made during the day serve the purpose of aggregation, while calls made in the evening are specifically employed for locating potential mates.

Sullivan et al. (2022) concluded that further investigation is required to fully understand the calling behaviours of PVH, but once this is understood, playback experiments similar to those used by Mazzoni et al. (2009b; 2017) and Gordon et al. (2017) could be used to assess their potential applications as management tools. The transmission of specific disruptive signals across kiwifruit trellises for VMD, or the application of repellent vibrational signals to reduce the number of pests settling in orchards, are two possible applications which may provide significant economic impacts.

RESEARCH AIMS

The primary objective of the research presented in this thesis was to advance the comprehension of PVH behaviour. This was explored in three distinct but interconnected areas of study.

Firstly, I endeavoured to elucidate circadian patterns to the vibrational communication behaviour of PVH. The findings will not only deepen comprehension of PVH, but could also serve as a valuable resource for future researchers who wish to further study their communication for pest control, such as VMD.

Secondly, I sought to examine the phenology of PVH, with particular emphasis on their emergence as adults and the potential for sexual bimaturism.

Finally, I investigated the preferences of PVH towards different plants with the aim to establish a hierarchy of plant preference, the implications of which could be informative for intercropping strategies.

CHAPTER 2: CIRCADIAN PATTERNS OF THE VIBRATIONAL COMMUNICATION BEHAVIOUR OF PASSIONVINE HOPPERS

BACKGROUND

Circadian rhythms are regulated by internally-generated autonomous clocks that are synchronized or entrained by environmental cycles. Their study (chronobiology) is an active area of research in humans and other animals because these rhythms play a crucial role in regulating the timing of various activities, physiological processes, and behavioural patterns (Nation, 2022a). Daily cycles of behaviour can be moderated at a genetic level through endogenous clocks, and through exogenous cues such as light and temperature, which are often referred to as zeitgebers (German for timer) (Tauber et al. 1986; Sakai & Ishida 2001; Nation, 2022a). Endogenous clocks are controlled by 'clock genes', which work on a transcriptional level to produce proteins that interact in feedback loops to generate the oscillating pattern of a circadian rhythm (Saunders et al., 2002a; Tataroglu & Emery, 2015). The function of these genes is subject to entrainment from external cues, such as the photopigment CRY (*cryptochrome*) which is sensitive to blue light and plays a critical role in resetting internal clocks in *Drosophila* (Emery et al., 2000).

The release of these proteins has been especially well studied in *Drosophila melanogaster* (Saunders et al., 2002a; Tataroglu & Emery, 2015). The process begins when two proteins, Clock (CLK) and Cycle (CYC), form a complex. This CLK-CYC complex binds to the promoter regions of two key clock genes, period (*per*) and timeless (*tim*), activating their transcription. Next, the *per* and *tim* genes are transcribed into mRNA and translated into PER and TIM proteins, respectively. Initially, these proteins are unstable and prone to degradation but after a series of post-translational modifications and interactions with other proteins, PER and TIM become stable. They form a complex (PER-TIM) which moves back into the nucleus and inhibits the activity of the CLK-CYC complex. This, in turn, inhibits the transcription of PER and TIM, forming a negative feedback loop that causes levels of PER and TIM to decrease. At dawn, light leads to the degradation of the TIM protein, which in turn results in the degradation of the PER protein. This degradation resets the clock and allows the CLK-CYC

complex to activate the transcription of once again PER and TIM, starting a new circadian cycle.

Coordinating behaviour with regular intervals is particularly important at the population level, where it ensures the effective functioning of the entire group. In particular, within-species synchronization of mating activity is vital to reproductive success (Sakai & Ishida, 2001). Various components of reproductive behaviours in some insects, as noted by Steel and Vafopoulou (2002), have been found to follow circadian rhythms, incorporating both exogenous and endogenous elements. Internal rhythms control the timing and coordination of mate seeking behaviours. However, the actual initiation of copulation can be contingent upon the presence of suitable lighting conditions, often occurring during the dim light of dawn or dusk.

Dawn and dusk are commonly utilized zeitgebers as they are more reliable than cues that may be affected by weather fluctuations, such as temperature and humidity (Fleissner & Fleissner, 2002). Aschoff's rules propose that diurnal animals primarily rely on dawn as a zeitgeber, while nocturnal animals use dusk as their primary time cue (Saunders et al., 2002b; Beaulé, 2008). To test this rule, animals can be subjected to constant light conditions, which results in diurnal animals exhibiting an increase in the frequency of their circadian rhythms (i.e., a shorter rhythm), while nocturnal animals display a decrease in the frequency of their oscillations (Beaulé, 2008). While Aschoff's rules appear to apply to most animals (Beaulé, 2008), there are some exceptions. One insect that breaks these rules is the cabbage looper (*Trichoplusia ni*), which although being nocturnal, has been shown to always reach peak calling activity 20-21 hours after dawn regardless of when the scotophase (the dark portion of a day-night cycle) occurs (Sower et al., 1971; Levi-Zada & Byers, 2021).

The process of signalling to advertise to mates is one aspect of mating-related behaviour that frequently exhibits a circadian rhythm in insects. By aligning their reproductive behaviours and physiology with the appropriate time of day or night, insects can increase the efficiency and success of their mating encounters. For example, in their review, Levi-Zada and Byers (2021) point out that concentrations of mating-related pheromones in four species of female moths followed circadian patterns, and that timing of mate seeking, and courtship behaviours are closely related to the peaks of these concentrations.

The aim of the following experiment was to describe the circadian rhythm of PVH vibrational calling behaviour. So far, the only study describing PVH calling behaviours conducted 30 min recordings of PVH in fully lit conditions during the day (Sullivan et al., 2022). Consequently, they were unable to draw any conclusions relating to daily cycles in vibrational behaviour or behaviours associated with scotophase. A more complete record of adult PVH daily behaviour patterns can be formed by undertaking 24-hour vibration recordings. Importantly, this will inform future researchers of the optimal times to record vibrational communication.

I hypothesised that peak calling activity would occur around dusk. This was based on anecdotal observations from researchers working with PVH (David Logan, pers. comm.), and assertions from both Steel and Vafopoulou's (2002) and Saunders et al.'s (2002b) work suggesting that insect mating often occurs at this time.

METHODS

INSECT REARING

From December 2021 – February 2022 and December 2022 – February 2023, wild PVH nymphs (N ~ 2,000-5,000) were collected weekly in Te Puke, New Zealand, and shipped to Plant & Food Research, Lincoln, New Zealand. These were reared in a temperature and light-controlled room inside 45 x 45 x 45 cm mesh cages (BugDorm, MegaView Science Co., Taiwan). Each week, ~1,000-2,000 nymphs were added to replenish these populations. Additionally, insects collected from colleagues' gardens around Christchurch were used to supplement the population.

To simulate summer day and night cycles, the room was lit with 8 full-spectrum lights on a 15:9 light/ dark cycle. Sunset and sunrise were simulated by turning each light off/on 15 min apart. The temperature in the room was set at approximately 23°C during light periods and 14°C during dark periods. This lighting and temperature regime was chosen to best mimic the average outdoor conditions for Te Puke from November to February (Chappell, 2013).

In the rearing cages, nymphs were provided with planted *Griselinia littoralis* saplings for food, as this has been shown to be an adequate food source (Sullivan et al., 2022).

Additionally, their feeding was supplemented with *M. ramiflorus* cuttings, as nymphs reared on it had the highest survival rates in the study by Logan et al. (2002).

As adult insects emerged, they were separated into a 45 x 45 x 45 cm mesh cage (BugDorm, MegaView Science Co., Taiwan), and likewise provided with *G. littoralis* saplings and *M. ramiflorus* cuttings.

VIBRATION RECORDING SET-UP

The recording set-up was similar to that used by Sullivan et al. (2022). The recording room was lit using two full-spectrum lights and sound-dampened using acoustic wall panels, rubber insulating pads on the feet of the tripod that supported a laser vibrometer (PDV 100, Polytec, Waldbronn, Germany), and a vibration-isolated table. I recorded vibrations made by adult PVH using the laser vibrometer with the beam focused on a piece of reflective tape (~2 x 2 cm) adhered to the vein on the abaxial side of a *G. littoralis* cutting (Figure 4). The cutting was held taut between two modified Petri dishes (Figure 4(a)) with its stem suspended in a container of water (Figure 4(d)), both of which were held upright using a retort stand (Figure 4(e)). PVH were enclosed inside the modified Petri dishes. The Petri dish facing the laser had a hole drilled in its centre to allow the laser to pass through but was not big enough to allow any PVH to escape (Figure 4(b)).

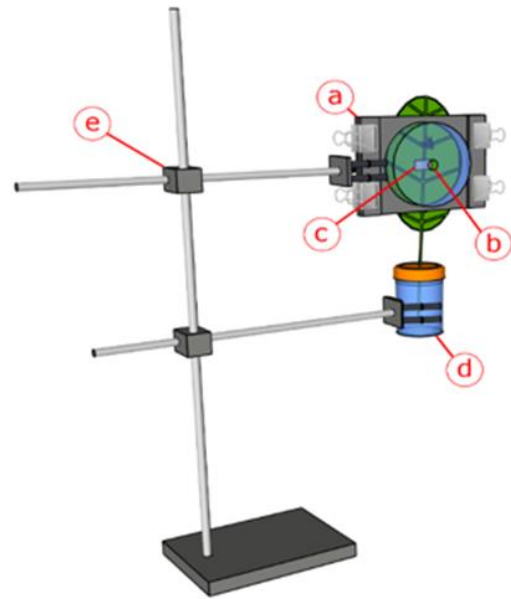


Figure 4: 3D rendering of recording set-up. a) two Petri dishes set inside plastic frames, held together by bulldog clips, b) a small hole drilled in the centre of the Petri dish facing the laser, c) ~2x2 cm reflective tape adhered to the abaxial side of a leaf, d) container of water with leaf stem suspended inside, e) retort stand.

Recordings took place in February 2022 and from December 2022 to April 2023. I recorded groups of three adult males and three adult females of mixed ages. To ensure subjects were naïve I did not reuse PVH between experiments. Each recording lasted 24 hours. To avoid damage from overheating, the laser vibrometer was shut off for at least 30 minutes between recordings. This also allowed time for the next recording to be set up.

However, this meant I was not able to start recordings at the same time each day. The recordings were digitized using Raven Lite 2.0 (The Cornell Lab of Ornithology, Ithaca, NY, USA) with a sample rate of 48,000 kHz and a 24-bit resolution. For the duration of this experiment, the photophase in the recording rooms began at 06:00 NZDT, and scotophase at 21:00 NZDT.

ANALYSIS

I conducted 18, 24-hour recordings in total. For every replicate, I calculated the percentage of time that was spent calling in half-hour blocks (i.e., 48 blocks for each 24-hour recording). The duration of calls was calculated by measuring the seconds a call train (Figure 5; Appendix 2) lasted. If a call train covered more than one half hour block, only the portion of the call train within each block was counted. A preliminary review of the data showed a non-linear relationship between the time of day and the mean amount of time the insects spent calling. Therefore, for my analysis, I utilised a generalised additive model with a quasi-binomial error structure using R version 4.0.5 (R Core Team, 2021). Because I was looking at proportions, I chose to use a quasi-binomial error structure. This treats proportions as ‘successes’ or ‘failures’, in this case success were the amount of time spent calling, and failures were the amount of time not spent calling in each half-hour block.

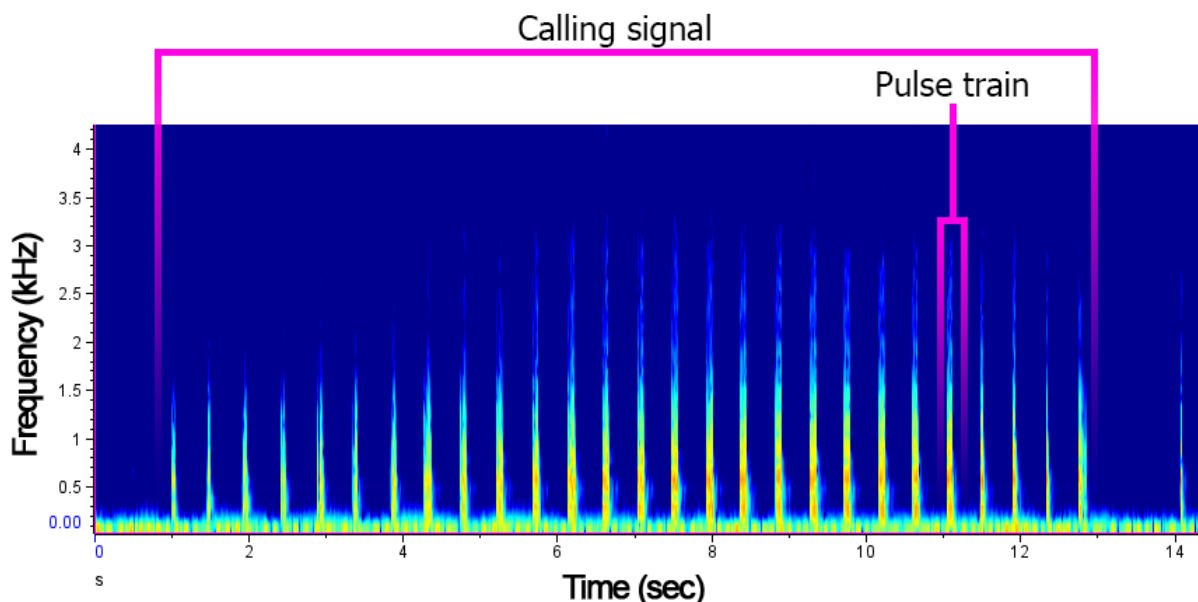


Figure 5: An example spectrogram of a calling signal taken from a recording I performed for this experiment. This calling signal is most similar to the male call described in Sullivan et al. (2022) (Appendix 1).

This model compared the proportion of time spent calling each half hour for the 18 recordings (the dependent variable) against smoothed functions for time of day and recording

number (predictor variables). Because time of day is a cyclical pattern (i.e., each day begins and ends at midnight), the time-of-day variable was converted into two smooth functions – one for cosine and another for sine – following a technique known as harmonic regression. By mapping each time point to a point on the unit circle using these trigonometric functions, I created a cyclic representation of time. This approach enabled the model to capture the repetitive nature of daily patterns, with the pattern cycling back on itself similar to the cyclical behaviour of sine and cosine function.

RESULTS

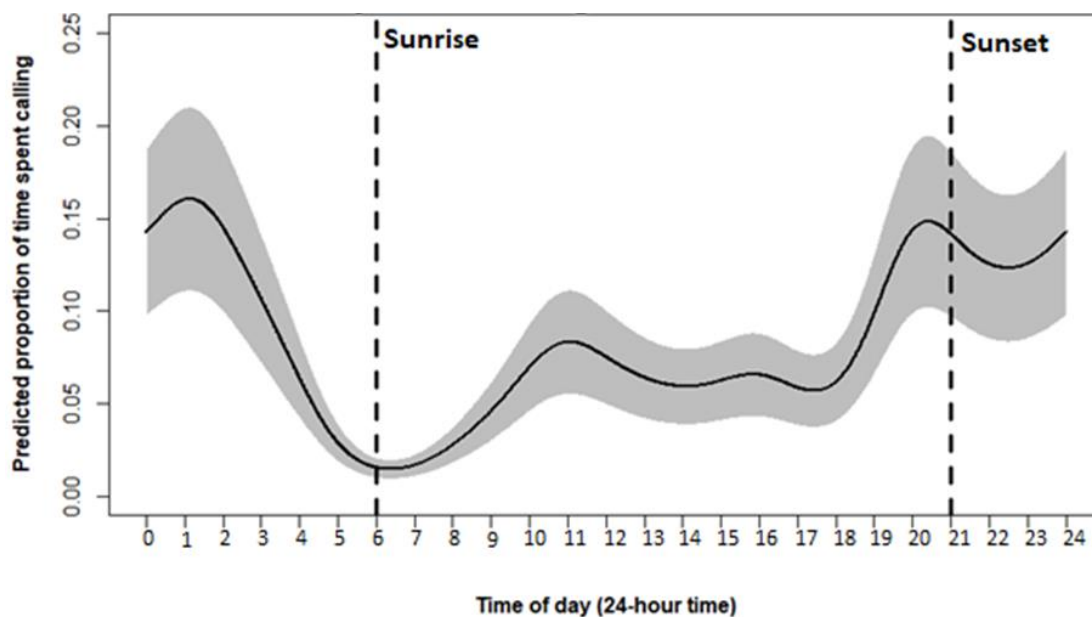


Figure 6: Generalised additive model showing the predicted proportion of time spent calling by adult PVH over a 24-hour period. The grey area surrounding the spline (solid black line) represents its 95% confidence interval. Two dashed, vertical lines indicate the time sunrise and sunset occurred.

A plot of the generalised additive model (Figure 6) predicts that adult PVH are most likely to call between 19:00 and 02:30, with the highest proportion of time spent calling being ~16% at 01:30. After this, the proportion of time spent calling dropped gradually to ~3% at 06:00. Calling activity then increased to ~8% at 11:00 whereafter it plateaued until 18:00 after which it increased until ~14% at 20:00. A summary of this model (Table 1) shows a significant ($p < 0.001$) relationship between time of day and the proportion of time spent calling. However, it also reveals that this model only explains 50.7% of the deviance.

Table 1: Summary of generalised additive model.

Parametric coefficients				
	Estimate	Std. Error	Z value	Pr(> z)
(Intercept)	-2.578	0.370	-6.975	<0.001

Approximate significance of smooth terms				
	edf	Ref.df	Chi.sq	p-value
s(costime)	3.943	3.993	23809	<0.001
s(sintime)	3.940	3.993	15868	<0.001
s(recording)	16.997	17.000	148853	<0.001

R-sq. (adj) = 0.474

Deviance explained = 50.7%

-REML = 139080

Scale est = 1

n = 863

DISCUSSION

My hypothesis, that peak calling activity would be seen around dusk, was only partially true. While dusk (21:00) occurred during the block of time where calling was most likely to be observed, this period lasted from 19:00 to 02:30, with the highest probability occurring at 01:30. This indicates that dusk does not act as a cue for the initiation of calling in PVH.

The results of the generalised additive model indicated that time of day is significantly correlated with the amount of time adult PVH spent calling. However, the model also showed that time of day only explained about half of the deviance in the amount of calling throughout a 24-hour cycle. Other environmental cues, such as temperature or humidity, can serve as additional zeitgebers and may have contributed to the remaining deviance (Nation, 2022a). For example, in the Emei music frog (*Nidirana daunchina*), calling activity is positively correlated with temperature and negatively with humidity, indicating that both factors act as zeitgebers, influencing the circadian rhythm of calling behaviour (Cui et al. 2011). If this study were to be repeated, inclusion of temperature and humidity measurements in the recording room would be useful for testing the effects of these variables on PVH calling behaviour.

Sullivan et al. (2022) observed an increase in the number of calls they recorded during the duration of their recording time, which lasted from 09:00 to 16:00. However, my results showed that calling activity throughout this time plateaued. This may have been due to

differences in methodology; Sullivan et al. utilized a 13:11 light/ dark cycle in the rooms they used to rear their PVH, and recorded individual females (n = 33), males (n = 54), and male-female pairs (n = 12). They also recorded single individuals and measured the duration of call signal lengths rather than the proportion of time spent calling. As I utilized the same location to rear the insects, differences in the duration of photoperiods, the number of PVH being recorded, and the types of data we were collecting would be the most likely difference between our experiments. The differences between our findings may also provide some insight into whether or not PVH use dawn or dusk as a zeitgeber.

As discussed in the introduction of this chapter, the timing of light exposure is a key zeitgeber in the circadian rhythms of many insects. According to Aschoff's rule, most diurnal animals will initiate circadian patterns in behaviour based on the occurrence of sunrise, while nocturnal animals use sunset as a zeitgeber (Saunders et al., 2002b; Beaulé, 2008). However, it is possible for some nocturnal insects to break this rule. Female *T. ni* begin calling activity around 20 hours after sunrise, regardless of the light: dark ratio they are kept in (Sower et al., 1971; Levi-Zada & Byers, 2021). As Sullivan et al. (2022) used a shorter photoperiod, and did not mention when their lights on period began in their methods, comparisons of our findings cannot indicate whether PVH are triggered by sunrise or sunset.

Throughout the day, the confidence intervals around the modelled spline were relatively wide, implying some uncertainty in the predicted amount of calling for most points in time. This suggests that the amount of calling may be subject to substantial variability and may be potentially influenced by other unaccounted factors. A noteworthy exception was observed leading up to 06:00. Between 01:00 and 06:00, the confidence interval sharply narrowed, indicating greater precision in the model's estimate at this time point. Concurrently, a significant decrease in the amount of calling was observed during this period. A less steep reversal of this pattern occurred immediately preceding 06:00, where the predicted proportion of time spent calling and the breadth of the confidence interval increased up until 11:00. These findings suggest that early mornings are a period of consistently low calling activity, an insight that might have important implications for understanding the overall calling behaviour.

A similar pattern can be seen in the circadian rhythm of locomotor activity of the house cricket (*Acheta domesticus*) (Figure 1Figure 7) under a 12:12 light/ dark cycle

(Cymborowski, 1973). Locomotor activity in this cricket sharply decreases some hours before dawn, and reaches its lowest levels at sunrise, after which activity slowly picks up throughout the photophase and then steeply increases towards dusk, remaining high throughout the scotophase. Interestingly, this study also found that under constant darkness, their free-running period shortened (with a few exceptions), indicating that this species is nocturnal according to Aschoff's rules (Beaulé, 2008).

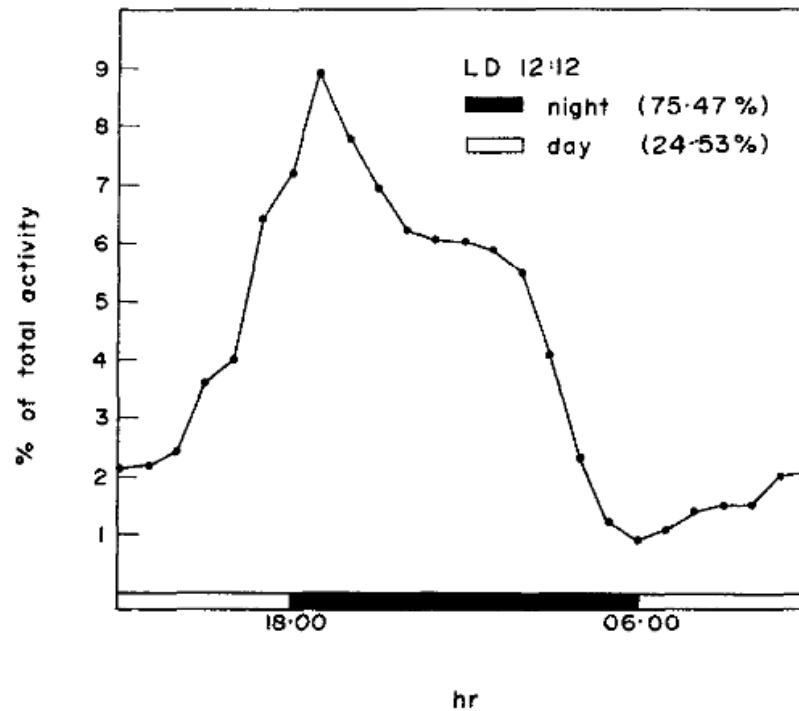


Figure 7: (Cymborowski, 1973) "Spontaneous locomotor activity of *A. domesticus* cultured under LD 12:12 conditions. A curve represents average percentage distribution of locomotor activity of 10 insects during a 24 period. Start of the dark period 18:00 hr, ended at 06:00 hr."

The addition of these findings somewhat complicates the idea that sunrise serves as a zeitgeber for PVH. On the one hand, the immediate increase in calling activity after sunrise lends credence to it being a trigger, paired with the difference in the timing of activity patterns between this study and Sullivan et al. (2022). On the other, the sudden decrease of calling activity begins at approximately the mid-point of the scotophase (five hours after sunset, and five hours before sunrise) and the similarities to another nocturnal insect make things less clear. If it is true that PVH use sunrise as a zeitgeber, the decrease in activity could be due to oscillating feedback loops controlled by the release of proteins by clock genes allowing for the timing of processes without immediate external triggers initiating them through various

interacting cycles of protein accumulation and degradation (Saunders et al., 2002a; Bloch et al., 2013; Tataroglu & Emery, 2015).

The overarching activity patterns of *S. titanus* are also akin to those of PVH, marked by heightened nighttime activity levels and subdued daytime levels. Nonetheless, it's noteworthy that the peak period of calling activity in *S. titanus* commences at twilight (Mazzoni et al., 2009c), unlike PVH, which initiates prior to twilight.

The most effective way to test my hypothesis – that PVH are diurnal – would be to expose them to free-running conditions. This means placing the insects in either constant light or dark conditions to see how their internal clocks operate without zeitgebers. According to Aschoff's rules, I would expect to see the pattern I observed in this study to become shorter and increase in frequency under constant light conditions (Beaulé, 2008).

CHAPTER 3: PHENOLOGY AND SEX RATIOS OF ADULT EMERGENCES IN *SCOLYPOPA AUSTRALIS*

BACKGROUND

Phenology is the scientific study of the timing of recurring events in biological life cycles. It focuses on understanding the temporal patterns of these events and their relationship with weather and climate conditions (Schwartz, 2013). It is similar in many ways to the study of circadian rhythms (chronobiology, discussed in detail in Chapter 2), as both relate to the timing of biological events and are controlled through exogenous cues. However, phenology focuses on patterns occurring on a larger temporal scale, such as seasons and years. The utilization of external cues to coordinate behaviour within a population is often crucial for biological functioning. A well-known illustration of this phenomenon is observed in many plant species, which employ phenological strategies in relation to their reproductive processes (Tang et al., 2016). The synchronization of reproduction based on seasonal cues, such as changes in photoperiod lengths and occurrences of seasonal events like winter frosts, confers several advantages for reproductive success (Tang et al., 2016). Firstly, it ensures the availability of pollinators for flowering plants, whose presence is also influenced by phenology. Secondly, it promotes the simultaneous attainment of reproductive maturity among population members. Lastly, it facilitates the production of offspring under optimal environmental conditions (Fenner, 1998).

Phenological patterns are also seen throughout the insect world. One phenomenon that occurs in many species, and is the focus of the research in this chapter, is the annual timing of different life stages such as eggs, larva, pupae, and adults. Insects often synchronize their emergences with specific environmental cues, such as temperature, day length, or the availability of host plants (Mjaaseth et al., 2005; Nietschke et al., 2007; Salis et al., 2017). A notable example of synchronized emergence in response to environmental cues is observed in the cicadas of the genus *Magicicada*. These cicadas exhibit a periodical emergence pattern, with different generations of nymphs emerging from the ground simultaneously after spending 13 or 17 years in development (Williams & Simon, 1995). The timing of their emergence is influenced by annual temperature changes, as studies have shown a strong

correlation between average April temperature and emergence dates (Kritsky et al., 2005). Additionally, research by Heath (1968) revealed that the critical trigger for emergence is when the soil temperature reaches an average threshold of 17.89°C.

Sexual bimaturism – where the phenology of adult emergences differs between males and females – is observed in various species. In organisms with discrete generations, this can manifest as a difference in the timing of adult emergences between the sexes (Singer, 1982; Morbey, 2013; Teder et al., 2021). In their meta-analysis, Teder et al. (2021) examined patterns of sexual bimaturism in 192 species of insects, spanning twelve orders and sixty-five families. Their findings confirmed that protandry, where males emerge as adults before females, is the dominant form of sexual bimaturism in insects (occurring in 65% of insects surveyed). Their study revealed that the occurrence of protandry was commonly associated with species where females exhibited longer development times. This said, the direction and magnitude of sexual bimaturism can change rapidly between generations, likely due to the plasticity in larval development times, caused by increased sensitivity to adverse early-life conditions affecting females more than males (Teder et al., 2021; Teder & Kaasik, 2023). An example of protandry can be seen in the emergence dates and sex ratios of the spittlebug *Philaenus spumarius*. Two studies looking into this (Halkka et al., 1967; Bodino et al., 2019) found that male insects emerged earlier in the year than females. Bodino et al. (2019) posited that this may be due to male *P. spumarius* having shorter preimaginal development times (the stage of insect development immediately preceding the adult form).

The reason many insects have sexually dimorphic larval development times is often due to sexual size dimorphism (Teder, 2013). Most often, females go through a greater number of instars and have a higher adult body mass (Esperk et al., 2007), which in turn relates to increased fecundity, or the number of eggs that she can produce (Honek, 1993). Sexual size dimorphism has clear benefits for larger females, leading to its selection, but males being able to copulate with larger females also gain considerable advantages in terms of the number of sired offspring, although it follows that the degree to which these advantages can be imparted will be impacted by the dynamics of a species mating system. In polyandrous species, males mating with virgins will sometimes ensure that the male's sperm is more likely to be used for fertilization, leading to a higher chance of successful reproduction (Rodrigues et al., 2020). However, in species where females can store sperm from multiple males, the

advantage of first male mating may diminish, as the sperm of subsequent males may compete with the first male's sperm for egg fertilization, leading to sperm competition.

In the suborder Auchenorrhyncha – to which PVH belong – sexual size dimorphism where females are larger than males is common (Constant, 2005, 2006a, b, 2018; Rahman et al., 2011; Wang et al., 2020; Razak et al., 2023), although not always present (Constant, 2006a; Akmal et al., 2019). There have also been several studies that found instances of protandry in this suborder (Chuche & Thiéry, 2012; Hou et al., 2015; Xiao et al., 2023). Both *Laodelphax striatellus* (Xiao et al., 2023) and *S. titanus* (Chuche & Thiéry, 2012) exhibit some degree of protandry, but in both cases the degree of protandry was influenced by temperature during nymphal development.

Another predictor of protandry is environmental seasonality and discrete, non-overlapping generations (Morbey, 2013). Indeed, these two factors often co-occur, as many insect species with discrete generations can be found in temperate zones, as resources are not available year-round (Singer, 1982; Yamamura & Kiritani, 1998). Interannual variation in seasonal conditions can cause variation in development times (Teder & Kaasik, 2023). This, combined with female development times being more sensitive to adverse conditions (Teder & Kaasik, 2023), may also account for inconsistent degrees of protandry observed by Teder et al. (2021). Previous reports on the emergences of adult PVH in New Zealand have indicated a correlation between temperature and the timing of adult emergences (Cumber, 1966; Matheson, 1978; Hill & Steven, 1989). Hill and Steven (1989) report that adult emergences typically last from late December to April. They reach peak abundances from January to March in the range described by Cumber (1966), and in the Waikato specifically, Matheson (1978) reported them as being most abundant from February to April. However, neither paper made note on the sex ratios of PVH during these times, and whether they exhibited sexual bimaturism. It is also important to note that these findings may not be true for present day populations. As discussed in Chapter 1, it appears that the range of PVH has only recently expanded as far south as Christchurch, GBIF.org, 2023, Lloyd Stringer, pers. comm.), seemingly likely due to climate change. Although, it is important to keep in mind that data from GBIF may be inaccurate, and that there has not been a published survey on the ranges of PVH since Matheson (1978).

Here, I investigated whether PVH exhibit protandry. I hypothesised that PVH will exhibit protandry, because adult females are on average larger than males (Fletcher, 1979), and therefore are more likely to have longer preimaginal development times. Additionally, both the native and introduced ranges of PVH are considered temperate zones, and PVH are a species with non-overlapping generations (Fletcher & Anderson, 1980; Gerard, 1989; Logan et al., 2017), making them more likely to exhibit protandry (Morbey, 2013). My investigation into these phenomena could contribute to a deeper understanding of insect behaviour and ecology, aiding more precise prediction of insect population dynamics and their effects on agriculture. Additionally, the findings could be instrumental in developing effective pest management strategies.

METHODS

Rearing was as described in Chapter 2, and only details specific to this work are described. Each day, the number and sex of newly emerged adult PVH was counted, and these insects were removed into separate cages to be used in other experiments. In cases where it was not feasible to count new adults (e.g., weekends), an average was calculated based on the total number of adults counted on the following available day, which was never more than five days.

ANALYSES

Since the exact count of nymphs was not known, I chose to utilize the percentage of adults (both male and female) that emerged each day in relation to the total number of adults that emerged throughout the entirety of both seasons combined. Statistical analyses were conducted using R version 4.0.5 (R Core Team, 2021). First, I calculated the average number of insects emerging on the same date for both seasons. I then graphed the percentage of adult females against males emerging each day using Microsoft Excel (Microsoft Corporation, 2018). As my data was not normally distributed, I used a Wilcoxon rank sum test to compare patterns in female and male emergences. Finally, to ascertain if the number of males and females emerging each season was different, I performed two two-sided binomial proportions tests to compare the total number of males and females emerging each season.

RESULTS

The line graph (Figure 8) records the percentage of insects emerging each day that were male or female and shows that the numbers of males and females emerging each day were roughly the same. Further, although not identical, both lines follow similar trends. For example, both sexes peaked at around the 1st of February. Indeed, the result of the Wilcoxon rank sum test comparing the trends in male and female eclosion found no significant difference between these groups ($W = 3964$, $N = 90$, $p = 0.783$). Binomial tests revealed that in the first season, the total number of males and females emerging was not significantly different ($\chi^2 = 1.403$, $df = 1$, $p = 0.236$), but in the second season, there were significantly more males.

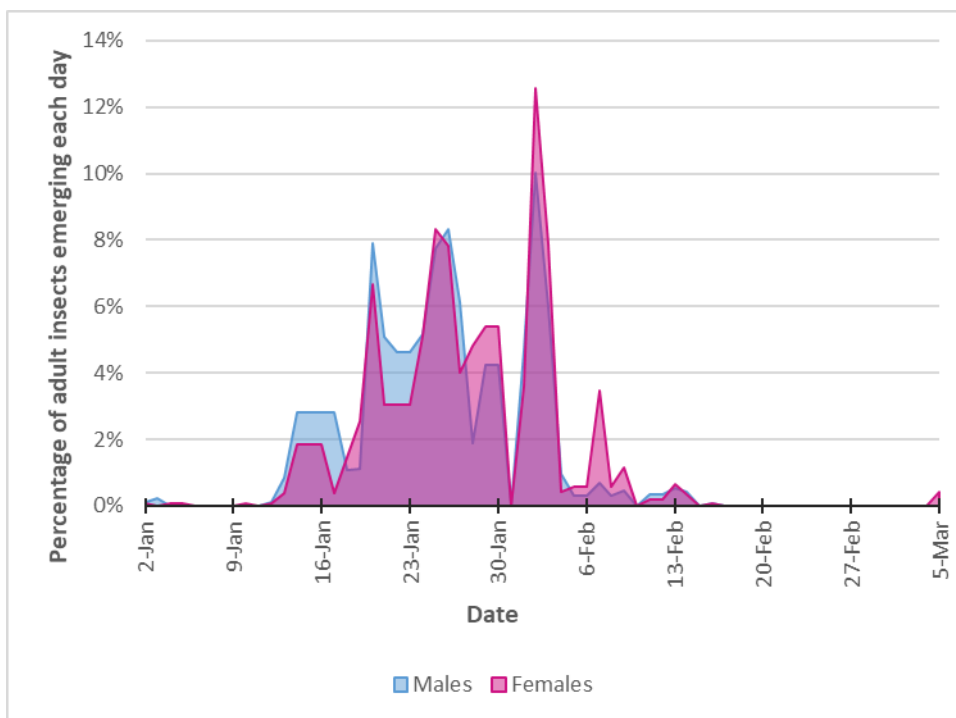


Figure 8: Percentage of male and female PVH emerging each day, calculated based on the average of the percentage of males and females that emerged during each season.

DISCUSSION

The results of my study did not support my hypothesis that PVH exhibit protandry. While the ratio of males to females differed significantly between seasons, possibly due to the greater number of insects used in the second season making differences in sex ratios more apparent, trends in the dates of their emergences did not. There are several possible reasons for this. Firstly, it is important to consider the effects of environment on their behaviour. As mentioned earlier, the phenology of adult eclosion is often controlled by external cues that follow seasonal changes. For example, climates gradually becoming warmer or colder, or photoperiods lengthening or shortening (Heath, 1968; Kritsky et al., 2005; Mjaaseth et al., 2005; Nietschke et al., 2007; Salis et al., 2017). In the laboratory where the insects in this study were reared, temperature and photoperiods were set at seasonal averages (Chappell, 2013) and did not change throughout the duration of the experiment. If it is the case that these changes act as cues for adult eclosion, their absence may have prevented protandry from occurring. Additionally, there is strong evidence that interannual variation in degrees of polyandry are caused by plasticity in female development times (Chuche & Thiéry, 2012; Teder et al., 2021; Teder & Kaasik, 2023; Xiao et al., 2023). If conditions in the laboratory that the PVH were reared in were favourable, especially in regard to female development, this may cause a lower degree of protandry.

To address these issues, future studies looking into at the emergence dates of PVH should be conducted *in situ*, over multiple years, while making a note of differences in environmental conditions. A similar study was conducted by Bodino et al. (2019), who surveyed the population phenology of several spittlebug species (Hemiptera: Aphrophoridae). These surveys were conducted in four olive groves in Italy from 2016 to 2018 to investigate spittlebug populations, utilizing quadrat sampling for nymphs and sweep net sampling for adults, alongside monitoring of air temperature and humidity (Bodino et al., 2019).

Alternatively, the effects of different environmental factors on sexual bimaturism could be simulated in a laboratory setting. Such a study would be difficult to carry out, especially since I and other researchers working with PVH (Nicola Sullivan. pers. comm.) experienced high, and unpredictable mortality rates when working with lab reared

populations, which often limited the number of available subjects to work with. However, such an experiment would allow for more precise control over variables of interest.

Another explanation is that male PVH may not benefit from earlier emergences. Modelling of adult male lifespans and the benefits of protandry show that protandry is only viable when males survive long enough for the emergence of females (Wiklund & Fagerström, 1977; Morbey & Abrams, 2004). Adult females of several species of auchenorrhynchs have been found to not emerge sexually mature (Mazzoni et al., 2009c; Nieri et al., 2017; Avosani et al., 2020). This is also found in *H. vitripennis*, the females of which take over 21 days post emergence to achieve sexual maturity (Sisterson 2008; Krugner, 2010). This delay may also be present in PVH. Although it has not been tested directly, Sullivan et al. (2022) observed male PVH beginning calling behaviours (possibly associated with mating) five to ten days post emergence as adults, and females calling from 11 to 28 days post emergence as adults. If males are unable to survive long enough to mate with sexually mature females, protandry would be disadvantageous. This said, I did not notice any difference in the lifespans of male and female PVH. Future studies investigating both the lifespans of adult insects and progression of sexual maturity in adults would be needed to assess this hypothesis. The latter can be studied in a comparable manner to Sisteron (2008), who performed dissections on adult female *H. vitripennis* of known ages to form a timeline of egg maturation schedules. An alternative method of testing sexual maturity would be through the use of vibrational playbacks of PVH mating communication to stimulate adult insects of known ages, similar to the approach adopted by Mazzoni et al. (2009c). However, such signals are as of now unidentified.

It is also important to reiterate that shipments of PVH for use in my experiments stopped after February for both seasons. Because of this, I cannot make any deductions as to the time period in which adult PVH emerge - only when they begin emerging. The last emergences recorded in this survey occurred during late February, however Hill and Steven (1989) note emergences occurring as late as April. Again, this would be easiest to address via *in situ* studies.

Understanding the phenology of insect pests can be vital to effective pest control strategies (Damos & Savopoulou-Soultani, 2010; Crimmins et al., 2020). Accurate and up-to-date information about the developmental stages of invasive species across their

geographical range can be crucial in making informed pest management decisions. This includes strategies such as early detection, eradication, suppression efforts, or implementing measures to slow the spread of the species (Herms, 2004). Understanding the timing of when invasive species transition between different life-cycle stages enables more effective monitoring activities. The use of phenological models for timing control actions to coincide with the peak susceptibility of the target organism optimizes effectiveness by targeting vulnerable life stages, reducing the need for excessive chemical use, saving time and resources, and minimizing any negative effects on non-target species (Herms, 2004). In PVH, knowledge of their phenology can be useful not only for future research into their behaviour, but specifically for the potential development of VMD (Mazzoni et al., 2009b), as it is only able to be used on adults.

CHAPTER 4: PREFERENCE HIERARCHIES OF *SCOLYPOPA AUSTRALIS* ACROSS MULTIPLE PLANT SPECIES: EFFECTS OF AGE AND SEX

BACKGROUND

Whether a phytophagous insect exhibits specialist or generalist attractions to different host-plants depends on a wide range of trade-offs. This is due to the fact that different host-plant species can offer varying fitness benefits to a specific species or population (Singer, 2007). In general, most phytophagous insects tend to specialize in one or a few host species (Jaenike, 1990). However, polyphagy, the ability to feed on multiple host species, is more commonly observed in species that are considered pests (Wan & Ni, 2016; Nyamukondiwa et al., 2022). Polyphagous species have an advantage in exploiting novel food sources (Bertheau et al., 2010), and their ability to metabolize a diverse range of chemical plant defences may contribute to the development of insecticide resistances (Hardy et al., 2017).

Even though polyphagous insects can utilize a broad range of host plants, they often exhibit preferences for specific plants. The ability to form both induced and innate preferences allows these insects to more efficiently locate reliable resources to increase their fitness (Jermy, 1985). The development of varying degrees of preferences in organisms attracted to multiple plant species leads to the formation of preference hierarchies. These hierarchies involve ranking different plant options in the insect's environment, with a prioritization of interaction with plants that offer the most suitable resources for specific behaviours.

Preference hierarchies are subject to a litany of selection pressures and trade-offs that often change throughout time and space. For example, high-quality plants may be uncommon or attractive to natural enemies, while common plants may be less nutritious. Further, parent-offspring conflict among polyphagous insects is potentially common. Ovipositing adults with different dietary needs to their offspring may result in a trade-off between optimised foraging for their own food, and optimal oviposition on hosts for their offspring (Scheirs & De Bruyn, 2002). According to Cunningham and West (2001), an ovipositing female's fitness should, in general, be proportional to the number of hosts she oviposits on multiplied by the quality of

her progeny. Therefore, while polyphagous insects can consume a wide variety of foods, their preferences reflect their evolutionary and environmental adaptations to optimize their nutrient intake and survival.

Understanding the preference hierarchies of pest species can provide important insight into the development of control strategies, specifically for intercropping. Intercropping is the practice of growing two or more crops together in the same field. It can be used as a management strategy for insect pests by creating a diverse agroecosystem that promotes natural pest control (Smith & McSorley, 2000). A more diverse habitat can reduce the concentration of a particular crop and make it harder for pests to find their host plants, which are dispersed among non-host plants. This makes it difficult for pests to find mates, lay eggs, or acquire resources necessary for survival. As a result, pest populations are lower and more dispersed in diverse cropping systems (Finch & Collier, 2000; Smith & McSorley, 2000). The 'Resource Concentration Hypothesis', originally posed by Root (1973), states that diverse crop stands are likely to deter insect pests due to them having less frequent encounters with appropriate hosts. By reducing the availability of preferred host plants, the pest dilution effect can limit pest outbreaks and reduce the overall impact of pest damage on crop yields.

Some plant species attract beneficial insects that can control pest populations, while others can repel or deter pests. By intercropping these species, farmers can promote the presence of natural enemies of pest insects, such as predators or parasitoids, while also deterring or repelling pest insects (Tscharntke et al., 2007; Letourneau & Bothwell, 2008). To illustrate this, *B. tabaci* (Hemiptera: Aleyrodidae), also known as the silverleaf whitefly, is a major pest of many crops worldwide. Intercropping has been shown to be an effective management strategy for this pest by promoting natural pest control and reducing the incidence and severity of whitefly outbreaks. *B. tabaci* are further discouraged by intercropping with unsuitable hosts through the aforementioned Resource Concentration Hypothesis (Root, 1973; Finch & Collier, 2000), such that *B. tabaci* are found at higher densities on tomato plants grown in bare soil compared to those grown alongside peanuts or coriander (Hilje & Stansly, 2008), with similar effects demonstrated for cucumbers (Zhao et al., 2013) and cassava (Gold et al., 1989) intercropped with less-preferred hosts (although one study on beans found intercropping to have no significant effect; Smith et al., 2001).

Intercropping can also aid in pest management through the effects of volatile organic compounds, which may repel the invader or hinder its ability to locate host plants. Carvalho et al. (2017) found that the volatiles of some aromatic plants were able to lessen the attraction of these insects to tomato plants in both laboratory-based Y-tube olfactometer experiments and field assays. Another study by Togni et al. (2010) examined the effects of tomato and coriander volatiles on the behaviour of *B. tabaci* using bioassays. They found that while the coriander volatiles did not repel the insects, they may be able to cover over the attractive tomato volatiles, which may explain why fewer *B. tabaci* are found in intercropped plots.

Intercropping has not yet been utilized for the management of PVH, however, understanding the specific nature of this insect's preference hierarchies may guide decisions on intercropping strategies for effective pest management in kiwifruit orchards. So far there has been one study looking into the preferences of PVH towards different plant species. Logan et al. (2002) surveyed native bush habitat in the Bay of Plenty, New Zealand, noting the presence or absence of adult and nymphal PVH. They then conducted choice tests on four commonly found plants known to harbour both life stages of the insect. These plants were *M. ramiflorus*, *P. excelsum*, blackberry (*Rubus* sp.), and Japanese honeysuckle (*Lonicera japonica*). Preference was measured by introducing groups of either nymphs or adult insects to cages containing these plants and counting the number of insects on each plant after ten days (nymphs), and seven and ten days (adults), as well as the number of scars from egg laying after 32 days. They observed strong attraction towards *M. ramiflorus* in both nymphs and adults. Furthermore, when reared on a single plant species, nymphs reared on *M. ramiflorus* survived best, and adults reared on wineberry (*Aristotelia serrata*) survived best and laid the most eggs (Logan et al. 2002), suggesting that the relative preferences PVH display towards the studied plants is influenced by the benefits they can provide them. This may account for PVH, in their nymphal stage, undergoing physical development which requires a diet high in protein, whereas adult males are fully developed soon after eclosion and no-longer require as much protein. Likewise, female insects tend to have higher protein requirements compared to males due to their reproductive physiology (Matthews & Matthews, 2009).

Melicytus ramiflorus and boysenberry (hybrid of various *Rubus* spp.) also have adaptive defences against insect feeding. *Rubus* species tend to produce a broad array of

defensive chemicals that make it difficult for generalist, phytophagous insects to feed (Gordon et al., 1997). Less information is available on the defensive capabilities of *M. ramiflorus*. However, Dewhurst (2012) reports that *M. ramiflorus* has a relatively high nitrogen content when compared to other plants used in their study, with nitrogen being an important, yet limiting, nutrient in all animals (White, 1978; Nation, 2022b). Interestingly, Dewhurst (2012) also found that *M. ramiflorus* had a low ranking in the preference hierarchies of tree wētā (*Hemideina* spp.), which are also polyphagous insects living in similar environments as PVH. Another example of plant defences, common in tomatoes, are trichomes, which serve as a vital defence mechanism in plants, by creating a physical barrier that makes it difficult for insects to navigate and feed. Some trichomes are sharp or sticky, while others produce chemicals that are toxic or repellent to pests. Through these combined physical and chemical defences, trichomes play an essential role in protecting plants from herbivorous insects (Kennedy, 2003; McDowell et al., 2010).

The aims of this study were two-fold. Firstly, by using nymphs of mixed sexes and instars, day old males and females, and two-week-old adult males and females, I investigated whether preference hierarchies in PVH of different ages and/or sexes differed. I hypothesised that there would be significant differences between the preference hierarchies of two-week-old males and females, as well as nymphs and all adult demographics, with the possible exception of two-week-old females. This is because two-week-old adult females might be under pressure to seek out hosts suitable for their offspring (Scheirs & De Bruyn, 2002). In other Auchenorrhyncha, females and males exhibit bimaturism in the development of their reproductive physiology post eclosion as adults where females reach sexual maturity later than males (Mazzoni et al., 2009c; Nieri et al., 2017; Avosani et al., 2021).

I then explored the preference hierarchies within each demographic. I investigated the foliage preference using three plants: tomato (*Solanum lycopersicum* 'Black Krim') boysenberry (hybrid of various *Rubus* spp.) and *M. ramiflorus*. *Melicytus ramiflorus* was chosen because it was previously found to be attractive to PVH (Logan et al. 2002). Logan et al. (2002) also found blackberries to be attractive to PVH; however, due to them not being available at the time of this study, I used boysenberry which are a hybrid of blackberries. *Solanum lycopersicum* plants were chosen because, during preliminary work, I observed PVH nymphs appearing to avoid settling on *S. lycopersicum* cuttings. Based on preliminary

observations of nymph behaviour, I hypothesised that relatively few PVH would settle on the *S. lycopersicum* cuttings. Logan et al. (2002) found that nymphs were more attracted to blackberry than adults, and that overall *M. ramiflorus* was the most preferred food source by both nymphs and adults. Based on this, I hypothesised that *M. ramiflorus* would be the most attractive plant among all demographics, and that boysenberry would be sought after by nymphs more so than adults.

My null hypotheses for this experiment were that there would be no differences in preference hierarchies between any of the demographics, and that there would be no significant differences in levels of preference towards the different cutting options.

METHODS

INSECT REARING

Rearing was as described in Chapter 2, and only details specific to this work are described. Adult males and females were reared together to increase the chances of observing the behaviour of mated females. For testing, I used nymphs of mixed sexes and instars, day old males and females, and two-week-old adult males and females. These demographics were chosen because they represented three distinct stages in the insect's life history. To simulate day and night cycles, both rearing and testing rooms were lit with 8 full-spectrum lights on a 15:9 L/D cycle. Sunset and sunrise were simulated by turning each light off/on 15 min apart. The temperature in the rooms was set at 23°C during light periods and 14°C during dark periods. This lighting and temperature regime was chosen to best mimic the average outdoor conditions for Te Puke from November to February (Chappell, 2013). As the nymphs were wild-caught, their previous diet was unknown. In their rearing cages, PVH were provided with planted *G. littoralis* saplings for food, as this has previously been established as an adequate food source (Sullivan et al., 2022) and was not used in my experiments, therefore would not introduce possible biases through induced preferences. Newly emerged adults were collected daily from the rearing cages using a flat-bottomed centrifuge tube and transferred into new 25 x 25 x 25 cm mesh cages (BugDorm, MegaView Science Co., Taiwan) separated by sex and date of adult eclosion.

CHOICE EXPERIMENT

Five demographics (nymphs, day-old males, day-old females, two-week-old males, and two-week-old females) were used for the choice experiment, with thirty replicates performed for each demographic. Each replicate consisted of five PVH of the same demographic, placed inside a sealed jar containing a cutting of each plant species (Figure 9). The set up for each replicate of the choice experiment consisted of 1.5 litre jar with two holes drilled into the top. One hole was covered in mesh to provide airflow, the other was used to introduce PVH into the jar, after which it is sealed with a cork. Inside the jar, ~15 cm long cuttings consisting of a stem and approximately equal area of leaves of *M. ramiflorus*, boysenberry, and *S. lycopersicum* were adhered to skewers with sticky tape for support. Again, using sticky tape, the cuttings were attached to the inner lip of the jar roughly equidistant apart. They were left in this set up for 24 h, after which the number of insects on each cutting, or on the sides of the container (referred to as null), were counted.



Figure 9: Diagram of testing apparatus

TRICHOME INVESTIGATION

In order to determine what trichome types were present on the variety of tomato used in the choice experiment I took cuttings from vegetative shoots and examined them under a compound microscope (Wild M5A, Wild Heerbrugg AG, Heerbrugg, Switzerland).

ANALYSIS

Statistical analyses were carried out using R version 4.0.5 (R Core Team, 2021). Firstly, I performed chi-square tests of independence between day-old males and females, nymphs and day-old adults, nymphs and two-week-old males, nymphs and two-week-old females, and two-week-old males and females to determine if there were any differences between the preference hierarchies of these groups. As I found no statistically significant differences between day-old males and females, these were combined for further analysis, including chi-square tests against nymphs, two-week-old males, and two-week-old females. While I found no statistically significant difference between nymphs and two-week-old females, these

groups were not combined due to them having considerable differences in their life-history stages. Next, I performed Kruskal-Wallis tests for nymphs, day-old adults (males and females, combined), two-week-old males, and two-week-old females to determine if any differences in preferences towards the cuttings within these groups were statistically significant. A Kruskal-Wallis test was used as the data in this experiment did not have a normal distribution of residuals. Finally, as all four Kruskal-Wallis tests showed significant differences, I used Dunn’s tests adjusted with the Bonferroni method to make pairwise comparisons between groups.

RESULTS

The results of the chi-square tests of independence (*Table 2*) showed that, except for day-old adult females and males and two-week-old females and nymphs, there were significant differences between groups in the total number of insects counted on each option.

Table 2: Results of chi-squared tests comparing the differences in the number of insects on each option.

Comparisons	χ^2	Df	p-value
Day-Old Males vs Day-Old Females	3.61	3	0.3071
Nymphs vs Day-Old Adults	18.05	3	0.0004 *
Nymphs vs Two-Week-Old Males	17.84	3	0.0005 *
Nymphs vs Two-Week-Old Females	2.26	3	0.5196
Two-Week-Old Males vs Two-Week-Old Females	10.02	3	0.0184 *

* $p < 0.05$

All Kruskal-Wallis tests performed on each group were significant, indicating that within each of the four groups tested, there was an overall effect of cutting type, with differences in the number of insects landing on at

Table 3: Results of Kruskal-Wallis tests performed on nymphs, day-old adults, two-week-old females, and two-week-old males

Group	H	df	p-value
Nymphs	21.804	3	0.001
Day-Old Adults	60.841	3	< 0.001
Two-Week-Old Females	37.977	3	< 0.001
Two-Week-Old Males	48.267	3	< 0.001

least some of the four options (*Table 3*). To determine the source of these differences, Dunn’s pairwise comparisons were carried out. These showed that amongst all demographics, *S. lycopersicum* was the least preferred option (

Table 4: Results of Dunn's tests with Bonferroni correction investigating differences between the numbers of PVH settled on Māhoe (*M. ramiflorus*), boysenberry, tomato (*S. lycopersicum*), or the container (null). Performed on nymphs (n=30), day old adults (n=60), two-week-old females (n=30), and two-week-old males (n=30).

). For nymphs and two-week-old females, *M. ramiflorus*, boysenberry, and null were equally preferred. In day old adults, boysenberry and null were most preferred, followed by *M. ramiflorus*. In two-week-old males, boysenberry was the most preferred option, followed by *M. ramiflorus* and then null. These preference hierarchies are visualised in Figure 10, which shows the percentage of insects in each demographic on each cutting type.

Table 4: Results of Dunn's tests with Bonferroni correction investigating differences between the numbers of PVH settled on Māhoe (*M. ramiflorus*), boysenberry, tomato (*S. lycopersicum*), or the container (null). Performed on nymphs (n=30), day old adults (n=60), two-week-old females (n=30), and two-week-old males (n=30).

Comparison	Nymphs		Day-Old Adults		Two-Week-Old Adults		Two-Week-Old Males	
	Z	p	Z	p	Z	p	Z	p
Boysenberry-Māhoe	-1.2438	1.0000	3.4016	0.0040*	-1.2306	1.0000	2.7347	0.0375*
Boysenberry-Null	-0.0426	1.0000	0.5708	1.0000	0.7156	1.0000	2.2203	0.1584
Māhoe-Null	1.2012	1.0000	-2.8308	0.0279*	1.9462	0.3098	-0.5145	1.0000
Boysenberry-Tomato	3.2052	0.0081*	6.9555	0.0000**	4.5964	0.0000**	6.8039	<0.0001**
Māhoe-Tomato	4.4490	0.0001**	3.5539	0.0023	5.8270	0.0000**	4.0692	0.0003*
Null-Tomato	3.2478	0.0070*	6.3847	0.0000**	3.8808	0.0006*	4.5836	<0.0001**

**p<0.0001

*p<0.05

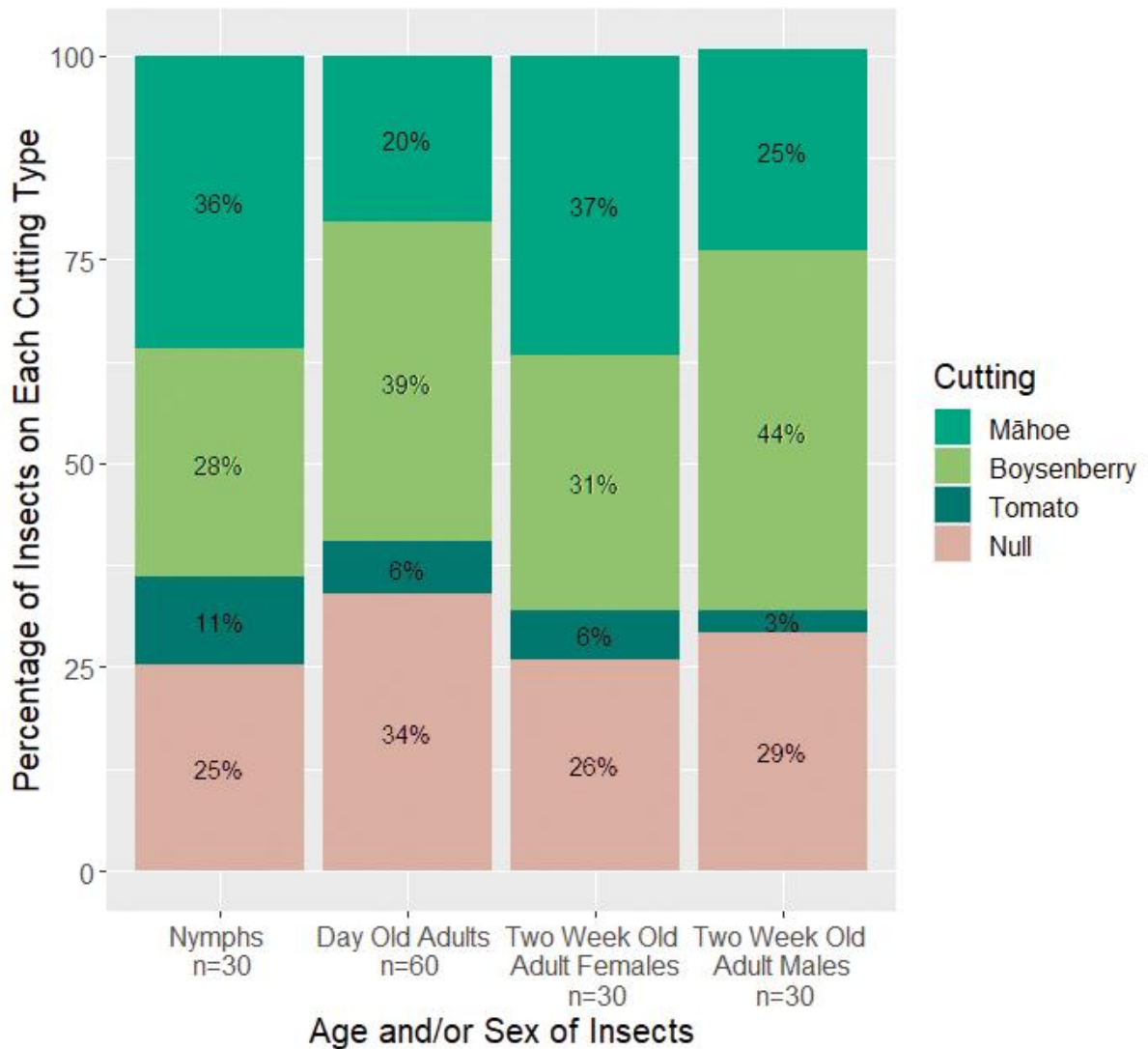


Figure 10: Stacked bar charts comparing the percentage of insects on each cutting type, or not on a cutting (Null), between nymphs, day old adults (males and females combined), two-week-old adult females, and two-week-old adult males. n = number of replicates.

DISCUSSION

These results unveiled distinct preference hierarchies within different demographics of PVH for various plants, underlining the role of both age and sex in these inclinations. I propose these differences may stem from varying nutritional requirements across different life stages, and in sexually mature females, a strategy to enhance offspring's survival and reproductive success.

NYPHHS AND TWO-WEEK-OLD FEMALES

It seems likely that the similarities I observed between nymphs and two-week-old females were due to the attraction of sexually mature females to host plants that would most benefit their offspring. This assumption is based on the possibility of the older females having

mated after being housed together with adult males for two weeks – two weeks being the typical commencement time for female mating (David Logan, pers. comm.). As highlighted by Cunningham and West (2001), ovipositing females can maximize their reproductive fitness by ensuring the optimal development and fitness of their offspring. This can be accomplished by laying eggs on food sources that are most suitable for their growth and development. However, evidence supporting this assumption outside of my experiment is unclear. In their study, Logan et al. (2002) tested both the longevity of, and number of eggs laid, by PVH in choice and no-choice experiments. They found both adults and nymphs would survive significantly longer on *M. ramiflorus* than blackberry, but they found no significant difference in the number of eggs laid on each of these plants. Hypothetically, this could be because blackberry plants provide other benefits to ovipositing females. For example, *M. ramiflorus* trees grow straight up and are relatively more exposed to the elements than a sprawling, thorny blackberry bush. Features of a plant's morphology, such as its fractal dimension (the space-filling properties of an object), leaf size, and amount of branching can all have significant impacts on predator foraging success (Reynolds & Cuddington, 2012).

Indeed, several studies have observed female insects being more attracted to protein-rich foods, as these provide the building blocks for physical development (Howse, 1974; Stockhoff, 1993; Cangussu & Zucoloto, 1995; Chapman, 1995; Barbehenn et al., 1999; Cornelius et al., 2000; Carrel & Tanner, 2002; Matthews & Matthews, 2009). Newer foliage tends to contain more protein (Matthews & Matthews, 2009). The *M. ramiflorus* cuttings used here were younger than the boysenberry, which could explain why two-week-old females were most attracted to *M. ramiflorus*, as this would provide the best source of protein for maturing nymphs.

TWO-WEEK-OLD MALES AND FEMALES

Conversely, male insects have been found to show a greater attraction to carbohydrates (Rusterholz & Erhardt, 2000; Carrel & Tanner, 2002; Prabhu et al., 2008). According to the Ghiselin-Reiss small-male hypothesis, a reason males are often the smaller sex in sexually size dimorphic species, is that having a smaller body demands less energy. Therefore, the male can dedicate more time to pursuing mating attempts rather than foraging (Blackenhorn et al., 1995; Mollet et al., 2023). Carbohydrates supply males with quickly available energy, which allows them to spend more time on mating related activity. If it is the

case that mated female PVH prioritize seeking host plants that maximize the fitness of their offspring, while sexually mature males prioritize feeding behaviours that enhance their ability to multiply mate, this could potentially provide an explanation for the significant differences observed between the preference hierarchies of two-week-old males and females.

DAY-OLD ADULT MALES AND FEMALES

However, this does not explain why day-old adults were the group least attracted to *M. ramiflorus*, as I expected that day-old-adults of both sexes may be more attracted to the younger (and consequently presumably more protein rich) *M. ramiflorus*, which is needed for sexual development. The reproductive development – and therefore fecundity – of day-old adult female insects is most often limited by protein availability. In other auchenorrhynchs, female calling activity and responsiveness to mating is positively correlated with the development of their ovarioles and the presence of mature eggs, whereas males are sexually mature soon after eclosion as adults (Mazzoni et al., 2009c; Nieri et al., 2017; Avosani et al., 2021). Males, require fewer resources in order to develop gametes and are instead limited by available energy in order to actively seek and compete for mates (Nation, 2022b). For still maturing females, nutrient requirements may be related to the development of ovarioles; but for males, who sexually mature earlier than females, nutrient requirements immediately post-moulting may be associated with extending their life span and in order to increase chances for mating. For these reasons, I had expected to see a higher attraction towards *M. ramiflorus* in day-old adults. Instead, they were most attracted to boysenberry which may have been higher in carbohydrate content. Perhaps, immediately post eclosion they require more carbohydrates to replenish the energy lost during moulting.

Alternatively, the near identical preferences of day-old adults may be due to them still being conditioned to seek the same food sources they did as nymphs. However, this seems unlikely, as the preference hierarchies of nymphs and day-old adults were significantly different.

MĀHOE AND BOYSENBERRY

Based on previous work (Logan et al., 2002), I had predicted that PVH would be most attracted to *M. ramiflorus*, yet in nymphs and two-week-old females, it was equally as preferred as boysenberry and the sides of the jar, and it was the second most preferred option for day old adults and two-week-old adult males. However, Logan et al. (2002) used

blackberry in their trials, and, while boysenberry and blackberry are closely related, there may be differences that affect their attractiveness. For example, this might be due to differing volatile profiles, as, although the range of nitrogenous compounds released by boysenberries and blackberries in response to herbivory damage is largely the same, the quantities released differ (Twidle et al., 2022), which in turn may affect behaviour.

TOMATO

While preferences towards *M. ramiflorus* and boysenberry differed between the demographics, *S. lycopersicum* was consistently the most undesirable option. Although tomatoes are a frequent victim to insect pests (e.g., *B. tabaci*), they possess several physical adaptations to deter such enemies. Trichomes – the ‘hairs’ growing on their stems – are a notable defensive adaptation. Kennedy (2003) describes type 4 and type 6 trichomes, which have been linked to higher resistance against arthropods. Microscopic examination of cuttings from the *S. lycopersicum* plants used in this study revealed that they possessed type 4 trichomes. Type 4 trichomes are densely packed and excrete potentially toxic exudate consisting primarily of acyl sucroses in *S. lycopersicum* (McDowell et al., 2010). Although reported as abundant on *S. lycopersicum* (Kang et al., 2010; McDowell et al., 2010), I did not find any type 6 trichomes on the portions of plant used in the experiment. It should be noted that this may be due to an error on my part, as the absence of these trichomes is unusual. It is possible, however, that they were absent due to some mutation, such as the *hairless* mutation described by Kang et al. (2010). The type 6 trichomes of *S. lycopersicum* produce large amounts of terpenoids; however, the exudate of type 6 trichomes are also known to entrap insects which may have actually caused some PVH to falsely appear to have settled on them if they were present (Kennedy, 2003). I also observed sparsely distributed type 1 trichomes. These trichomes are also glandular but produce much less exudate than types 4 and 6 (McDowell et al., 2010), and may play a relatively minimal role in herbivore defences.

One notable difference between tomatoes and the other tested plants is their release of particularly pungent volatiles. Plant volatile mixes can be found in the air around them, commonly referred to as the plant's headspace. These odours may provide insects with information used to guide behaviour from afar because headspace volatiles with light molecular weights can disperse large distances (Bernays & Chapman, 1994). Indeed, the volatiles of some tomato varieties have been found to repel other insect pests to varying

degrees. Bleeker et al. (2009) found specific terpenes in the headspace volatiles of wild tomato plants, including zingiberene, curcumene, p-cymene, α -terpinene, and α -phellandrene, repelled *B. tabaci*. Another study by Pérez-Hedo et al. (2021) found that when zoophytophagous mirids fed on tomato plants, they activated the release of herbivore induced plant volatiles (HIPVs), triggering both direct and indirect defence mechanisms. After exposure to specific HIPVs for 24-hours, the tomato plants in this study showed increased expression of defensive genes. Two of these HIPVs, (Z)-3-hexenyl propanoate and methyl salicylate, were further studied and found to make plants repellent to pests including *B. tabaci*, *Tuta absoluta*, and *Frankliniella occidentalis*, attractive to the parasitoid *Encarsia Formosa*. All of the volatiles identified in these studies have what are considered to be low molecular weights (>300 g/mol) (Dudareva et al., 2006) (NCBI, 2023a-i). These volatiles may be able to be used as a repellent to PVH, as found in other studies testing the utility of aromatic plants as deterrents in intercropping systems (e.g., Carvalho et al., 2017). Interestingly, the volatile profiles of *S. lycopersicum* consist mainly of terpenes (Raghava et al., 2010) which, as previously mentioned, are exuded mainly from type 6 trichomes, which I did not observe on the portions of plants used in this experiment. The fact that PVH were repelled from *S. lycopersicum* cuttings here indicates that either they produced terpenes through another structure, that they were being repelled through some other mechanism, or I that missed the presence of type 6 trichomes in my examination.

By including the proportion of insects that settled on the jar's sides (null), we can see that *S. lycopersicum* was not just the least chosen option, but that it was actively avoided. It is more likely that *S. lycopersicum* volatiles act as a repellent rather than masking the volatiles of *M. ramiflorus* and boysenberry, although a study similar to Togni et al. (2010)'s would be needed to test this.

CONCLUSIONS

It is important to note the limitations of this study. Firstly, further information on the nutrient profiles of the plants used would be necessary to back possible explanations I gave as to some of the preference hierarchies. For example, I posed that nymphs and two-week-old females were more attracted to *M. ramiflorus* than boysenberry due to the former possibly having a higher protein content. Another improvement that could be made is ensuring two-week-old females were actually mated. For the discussion of my experiment, I

worked under the assumption that two-week-old females were mated due to being housed with adult males past their assumed (and untested) age of sexual maturity. However, their mating status was not verified. In a future experiment, the oviposition preferences of gravid females could be tested in a similar manner to Logan et al. (2007), who counted the number of egg-laying scars left on different plants in a choice-test.

Given my overall results, *S. lycopersicum* plants may be a candidate for intercropping with kiwifruit as part of a pest management strategy. The aversion PVH display towards tomato, possibly due to the volatiles they release which can disperse into a wide area around the plant, may lessen the damage PVH cause to kiwifruit through the Resource Concentration hypothesis (Finch & Collier, 2000). Experimentally intercropping tomato and kiwifruit in the field (e.g., Hilje & Stansly, 2008), as well as testing the reactions of PVH to tomato volatiles (Carvalho et al., 2017) can be used to further investigate this. This said, it would be vital to ensure tomatoes are not hosts for other kiwifruit orchard pests before implementation.

CHAPTER 5: GENERAL DISCUSSION

SYNOPSIS OF MAIN FINDINGS AND INTERPRETATION

In this thesis, I conducted a series of experiments to delve into three different aspects of PVH behaviour. The primary aim was to contribute to the knowledge base and provide valuable insights for future researchers, particularly concerning their status as prolific and difficult to manage crop pests. By investigating these aspects, I aimed to enhance our understanding of PVH and pave the way for more effective management strategies in the future. Descriptions of a target species' behaviour are important to the development of novel and effective pest control methods, and is the first step of the Description, Identification, and Extermination (DIE) process constructed by Gordon and Krugner (2019). DIE was made specifically for the development of vibrational pest control and focuses on the description of vibrational calling behaviour and identification of calls that may be manipulated. However, the general concept can be applied to other approaches, such as intercropping. Here I will discuss these experiments and the implications that they may have on future research.

In Chapter 2, I explored circadian patterns in the vibrational calling activity of PVH, building upon previous work by Sullivan et al. (2022). I had predicted that peak calling activity would occur around dusk (21:00 in this study); however, I did not find this to be true. Rather, the highest proportion of time spent calling lasted from 19:00 to 02:30, with a peak around 01:00. Additionally, whilst I did find a significant influence of the time of day on the calling activity of adult PVH, this factor only accounted for about half of the observed variance in a 24-hour cycle, suggesting the potential influence of other environmental cues, such as temperature and humidity. Notable findings included a pattern of consistently low calling activity during the early morning, and substantial variability in the amount of calling throughout the day, possibly due to unaccounted factors.

These findings prompted discussion about PVH using dawn as a key zeitgeber, which is most typical of diurnal insects (Saunders et al., 2002b; Beaulé, 2008). However, the peak in calling behaviour occurring after dusk, decreasing activity observed at the scotophase midpoint, along with similarities in circadian patterns with the nocturnal *A. domesticus* (Cymborowski, 1973), complicates this proposition. Overall, my results lend support to the

hypothesis that PVH use sunrise as a zeitgeber. This said, this does not necessarily make them diurnal. Although it is uncommon, some nocturnal insects have been found to use dawn as a zeitgeber, therefore breaking Aschoff's rules (Beaulé, 2008). An example of this are *T. ni*, which reach peak calling activity 20-21 hours after dawn, that under normal conditions, would be during the scotophase. However, experiments that altered the ratios of light and dark periods they were exposed to reveal that despite being active during the night, they use dawn to set their internal clocks.

Understanding the circadian activity patterns of PVH is important for the development of pest control strategies for a few reasons. Firstly, it can aid future researchers in optimising their study methodologies, as they can anticipate the timeframes for observing calling behaviours. This predictive ability can be used in the next stage of the DIE process, which involves the identification of specific calls and their functional significance. By manipulating the light/dark cycles under which PVH are raised, researchers can concentrate their recordings on the periods of peak calling activity.

Secondly, this information could eventually enable pest control practitioners to fine-tune the timing of their interventions. Presently, vibrational pest control has primarily focused on disrupting mating behaviours (Saxena & Kumar, 1980; Mazzoni et al., 2009b, c, 2017, 2019a, b; Polajnar et al., 2014, 2015; Gordon et al., 2017; Gordon & Krugner, 2019). Future research pinpointing the times of day PVH are most inclined to engage in mating-related communication could enhance the efficacy of VMD techniques. Knowledge of circadian patterns of activity have already been utilized in the management of *S. titanus* in a field trial by Polajnar et al. (2016). Previous research had shown that *S. titanus* display a dip in flight activity during midday, and a peak in both flight and calling activity throughout the night (Lessio & Alma, 2004; Mazzoni et al., 2009c). In their trial, Polajnar et al. (2016) experimented with discontinuing VMD from 10:00 to 18:00 and found that this interruption did not diminish the effectiveness of VMD. It is worth noting, however, that insect populations subjected to such interventions might alter their activity patterns in order to counteract the impact of VMD (Mazzoni et al., 2019b). Mazzoni et al. (2019b) proposed that patterns of behaviour may not solely rely on photoperiod cues, but also climatic ones. By monitoring climatic factors, such as temperature and humidity, and identifying how these impact *S. titanus*'s behaviour (if they do at all), a more robust VMD system could be developed. I propose that similar studies could

be performed for PVH. As mentioned in the discussion of Chapter 2, factors such as temperature and humidity were not measured in my experiment. This potential alignment between intervention timing and natural behaviour could reduce the necessity for continuous treatment, leading to savings in time and resources.

In Chapter 3, I explored the hypothesis that PVH would exhibit protandry, but found that results did not support this idea. Despite observing significant seasonal differences in the male to female ratio, no differences were discerned in their emergence dates. The lack of protandry could be explained by male PVH not benefiting from earlier emergences, as theoretical models of male lifespan and protandry benefits suggest it is feasible only when males survive long enough for female emergence. In some species related to PVH, females do not emerge sexually mature, potentially causing delays for male mating opportunities. Therefore, if males cannot survive this delay, protandry becomes disadvantageous. What this would suggest, however, is that the species might benefit from earlier female emergences. This is because the first emerging males would be able to begin mating immediately after they eclose. Nevertheless, this may be offset by the fact female insects often go through more nymphal instars than males, potentially delaying their eclosion as adults (Esperk et al., 2007). All this said, to gain a more definitive understanding of the emergence patterns of PVH, a study looking into their emergences year-round would be useful.

Other factors may have contributed to this result, such as environmental influences like shifting climates and photoperiods that usually control adult eclosion, being absent in the laboratory setting where the study was conducted. Additionally, evidence suggests that the degree of polyandry could be influenced by variations in female development times which are, in turn, impacted by the favourability of the environment in which they develop (Teder et al., 2021; Teder & Kaasik, 2023). I suggested in Chapter 3 that multi-year, *in situ* surveys of PVH emergences could be performed in order to monitor the effects of environmental conditions on their phenology. Performing a survey such as this with the added perspective of the impacts of climate change may be vital to predicting future impacts of PVH. In Chapter 1, I briefly discussed how PVH have made a recent southward range expansion. Based on observations from previous surveys of PVH habitats (Cumber, 1966; Matheson, 1978), it appears that this may be in large part due to climate change. PVH are already a major crop pest for growers in the North Island of New Zealand, so gaining a more robust understanding

of what conditions are suitable for supporting their populations, and how this might allow them to further spread, is vital to their management. Additionally, understanding what time of year adult PVH are present will aid in the deployment of VMD.

Finally, in Chapter 4, I presented insights into how age, sex, and nutritional requirements influence the plant preference hierarchy in PVH. Distinct preference hierarchies were observed within different demographics (nymphs, day-old adults, two-week-old females, and two-week-old males). These differences may stem from varying nutritional requirements across different life stages or, in sexually mature females, a strategy to enhance offspring's survival and reproductive success. Despite these findings, there are certain limitations in this study, such as the lack of definitive information on the nutrient profiles of the plants used or the unverified mating status of two-week-old females. Future research could address these gaps and contribute further to the understanding of PVH plant preference hierarchies. Similarities in plant preferences between nymphs and two-week-old females were noted, and these could be due to the attraction of females towards host plants that would benefit their offspring. This aligns with the idea, supported by Cunningham and West (2001), that ovipositing females can maximize reproductive fitness by selecting optimal food sources for offspring's growth and development. This research also indicated that female insects are more attracted to protein-rich foods and males towards carbohydrates, a finding supported by various other studies. However, some results contradict these trends, suggesting a need for further research.

The consistent lack of preference for *S. lycopersicum* among all demographics was notable, and may be due to their physical adaptations, like trichomes, or due to the release of pungent volatiles that may act as repellents. *Solanum lycopersicum* (or another variety of tomato) might therefore be a viable option for intercropping with kiwifruit as part of a pest management strategy, given PVH's aversion to them. Tomato plants possess specific physical and chemical adaptations, such as trichomes and volatile organic volatiles (VOCs), which make them undesirable to various insect pests (Kennedy, 2003; McDowell et al., 2010; Bleeker et al., 2009; Pérez-Hedo et al., 2021). Additionally, by integrating tomatoes with other crops, the diversity of the agroecosystem can be enhanced, creating a more complex environment that might hinder PVH from locating their host plants. This strategy, rooted in principles of natural pest control, could not only reduce PVH infestations, but also foster a more sustainable and

environmentally friendly agricultural practice. Further research may explore the specific repellent mechanisms in tomatoes and how they can be most effectively utilized in different intercropping systems, allowing farmers to mitigate the impact of PVH on their crops. In combination with VMD, intercropping with *S. lycopersicum* could help reduce pest concentrations, leading to fewer mating opportunities. Indeed, intercropping with tomato has been found to reduce the abundance of flea beetles (*Phyllotreta cruciferae*) on collards (Tahvanainen & Root, 1972). This study found that odours from tomato plants interfered with the host-finding abilities of *P. cruciferae*. How exactly PVH locate host plants has not been studied. It is known that they are able to disperse long distances in order to locate hosts (Tomkins et al., 2000), but what senses are guiding them is currently unknown. It is likely olfaction plays some role in host location, as with other hemipterans (e.g., Chinta et al., 1994; Mazzoni et al., 2009a).

The role of olfaction in host finding for PVH, and their reactions towards different volatiles, including those produced by *S. lycopersicum* can be studied using behavioural methods such as olfactometer studies (e.g., Ying et al., 2003; Carvalho et al., 2017), where air from two sources is provided to the test animal in a Y-chamber; the animal then chooses which arm to choose based on the odour, providing behavioural evidence of attraction. Alternatively, the role of olfaction can be investigated at a mechanistic level using electroantennography (e.g., Chinta et al., 1994; Gemeno et al., 2006; Mazzoni et al., 2009a; Twidle et al., 2021). This technique measures the electrical activity in the neurons in an insect's antennae, and records changes in voltage that occur in response to different odours binding with olfactory receptor neurons. Electroantennography can be used in combination with olfactometer studies, as they inform researchers as to what volatiles PVH can sense. They can also be used to investigate how PVH perceive the interaction of *S. lycopersicum* volatiles and that of their hosts to see if they have a masking effect similar to those experienced by *P. cruciferae* (Tahvanainen & Root, 1972).

All of this said, a major concern I foresee with using tomato as a repellent is that it in of itself experiences high rates of herbivory from insect pests. Several studies I have previously mentioned, while discussing the concept of intercropping (Hiljje & Stansly, 2008; Togni et al., 2010; Carvalho et al., 2017), were investigating the use of intercropping to *protect*

tomato crops from insect pests. These studies investigated *B. tabaci*, a globally prolific, polyphagous pest that is present in New Zealand (although not widely established) (Scott et al., 2007). Although *B. tabaci* are not of major concern right now, this does highlight the importance of using an ecosystem-wide approach to pest management that considers how factors outside of a specific area of study might impact final results.

CONCLUSIONS

Although the findings of my studies do not provide information that could be immediately applied to control PVH, they do offer valuable information for the direction of future studies, including optimizing methodologies, and highlight knowledge gaps to be further elaborated upon. Through their recent range expansion, possibly caused by climate change, the threats posed by PVH to New Zealand's horticultural industries is escalating. The development of integrated pest management strategies such as intercropping and VMD are promising candidates for addressing the growing problem of PVH in New Zealand. These strategies, however, must be investigated further, and refined based on the unique ecological and environmental conditions of the regions they will be applied to.

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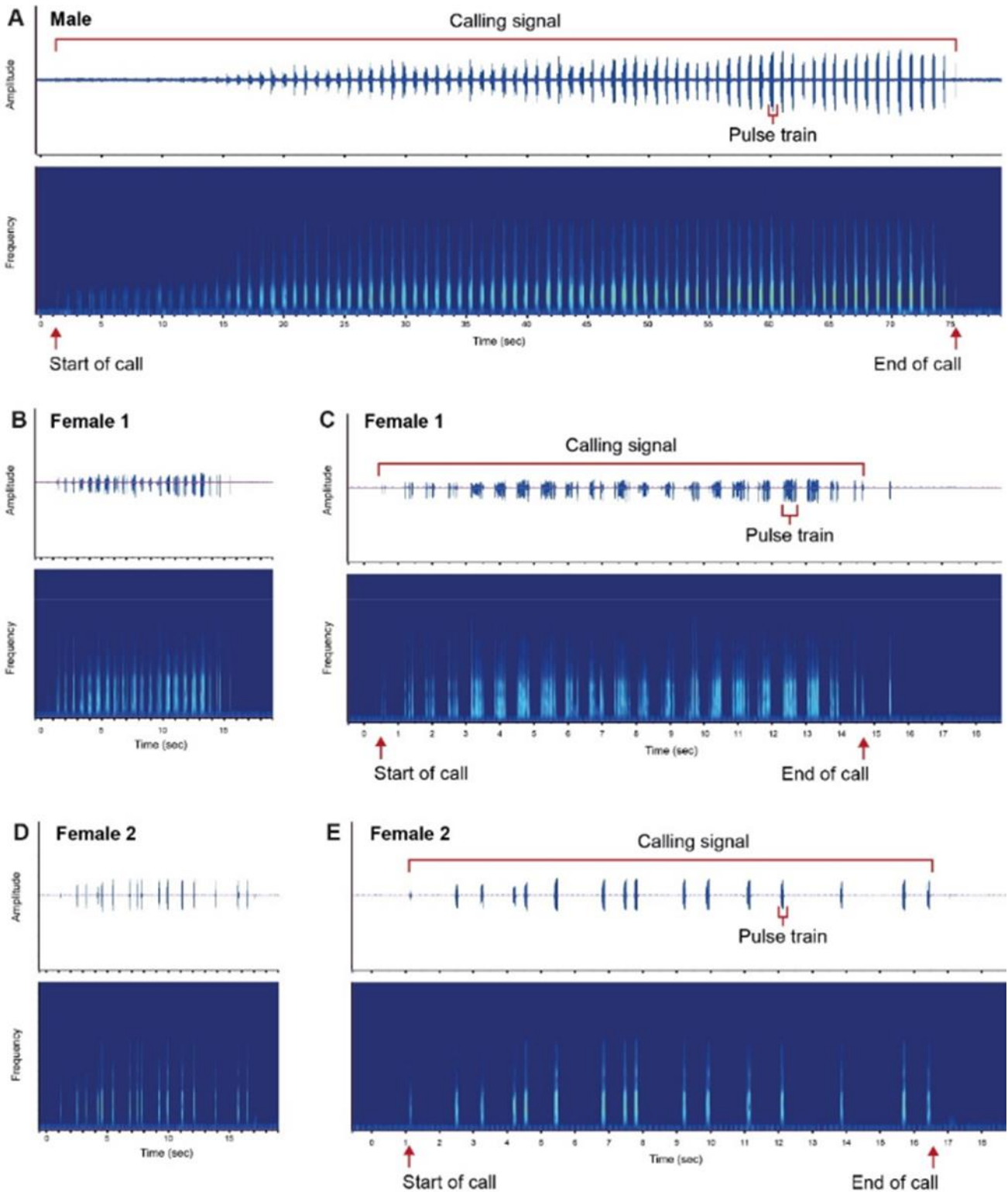
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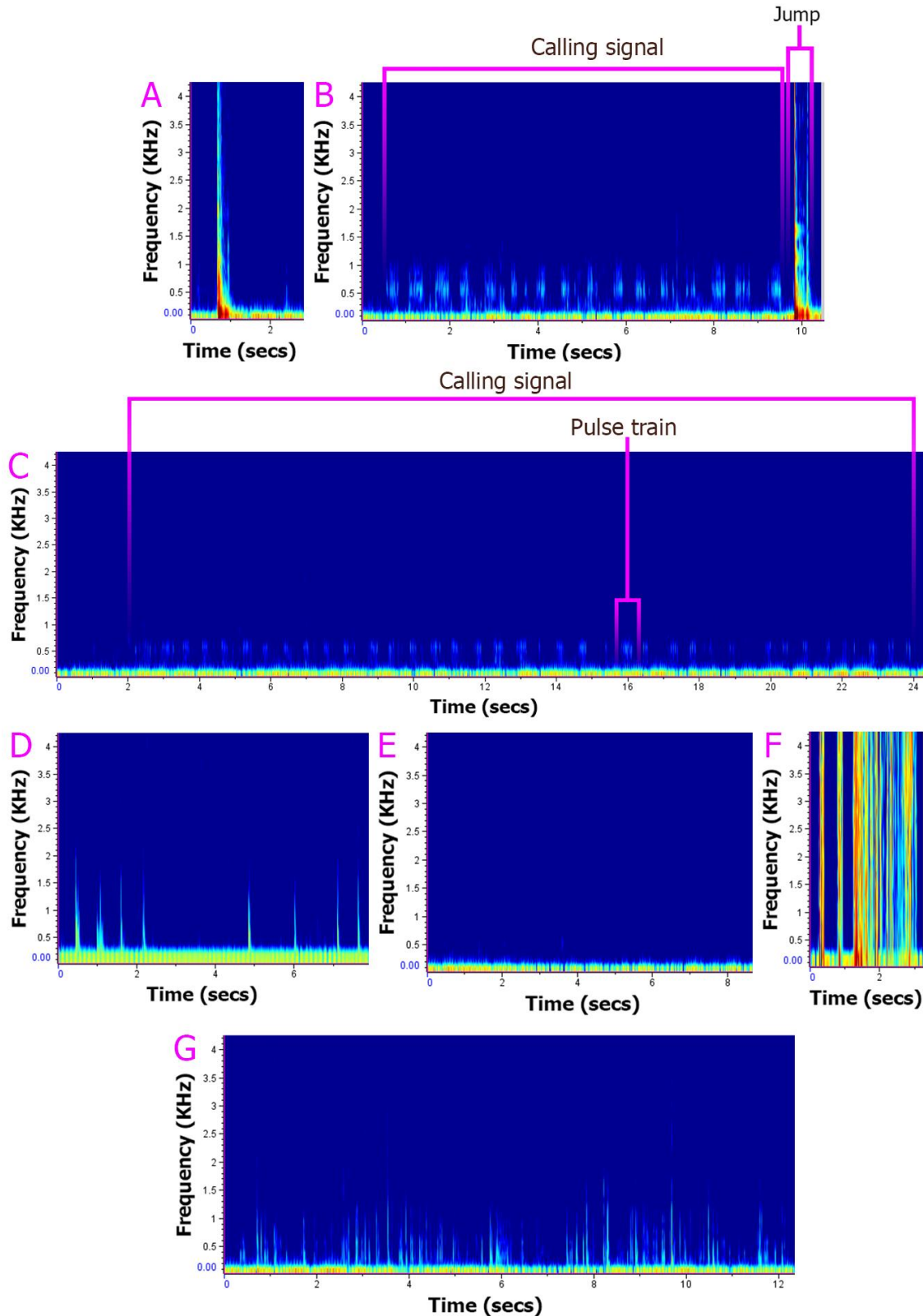
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APPENDICES



Appendix 1: Sullivan et al. (2022) Oscillograms (top) and spectrograms (bottom) of the identified calling signals of *Scolypopa australis* (A) male calling signal (B) female calling signal 1 at the same timescale as A & D, (C) female calling signal 1 on an increased time scale, (D) female calling signal 2 at the same time scale as A & B, (E) female calling signal 2 on an increased time scale.



Appendix 2: Spectrograms collected as part of Chapter 2. B, C, and D represent calls made by PVH. Calling signals in B and C have a lower maximum frequency than the one shown in Figure 5, and the duration of pulse trains are longer. They are most similar to the Female 1 call in Appendix 1. D shows sporadic pulse trains that do not form a typical, rhythmic calling signal. A and B both show the vibrations recorded when an insect jumps. E is a section of typical background noise, with no activity from the insects. F and G both show noise not made by vibrational communication or jumping. F is likely a result of an insect moving into the path of the laser. The cause of G is unknown.