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Research

Insecticide Responses in the Collembola Pest, *Sminthurus viridis* (Collembola: Sminthuridae), in Australia

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Abstract

Lucerne flea (*Sminthurus viridis* Linnaeus) is an important establishment pest of winter grain crops and pastures in Australia. Control of *S. viridis* largely relies on the application of insecticides through foliar sprays or seed treatments; however, in recent years, farmers have faced increasing difficulties managing this pest. This is likely due to their high inherent tolerance to certain chemicals, although there are increasing concerns around emerging resistance. Despite this, there have been no studies worldwide investigating insecticide sensitivity shifts on *S. viridis*. Further, there is currently no established method to test the response of *S. viridis* to neonicotinoids, which are now widely used to protect many crops attacked by this species. Here, we established a robust and sensitive bioassay methodology to test neonicotinoids against *S. viridis*. We also generated important sensitivity data for the first time across multiple *S. viridis* populations from geographically distinct regions in Australia to two commonly used insecticides, omethoate, and imidacloprid. While there was variation in responses between populations for both chemicals, there is no evidence to suggest insecticide resistance has evolved in the field. This study is an important step for future monitoring of insecticide resistance in *S. viridis*, particularly given the considerable selection pressure imposed on this pest in Australia and its purported high-risk of evolving resistance.

Key words: lucerne flea, chemical sensitivity, neonicotinoid, pest, resistance

The lucerne flea (*Sminthurus viridis* Linnaeus) is an economically important pest of winter grain crops and pastures in Australia. *Sminthurus viridis* attack a wide range of field crops and pastures, with broadleaf plants, such as subterranean clover and lucerne, particularly susceptible to feeding damage. They are also known to cause considerable damage to canola, wheat, barley, oats, and pulses (Bishop et al. 2001, Gu et al. 2007, Micic et al. 2008). *Sminthurus viridis* are most damaging at the establishment phase of plant development in autumn and again in spring when conditions promote high pest densities (Bishop et al. 2001, Roberts and Weeks 2011a). They are found throughout areas of southern Australia with a Mediterranean-type climate and are generally present from autumn to spring, where they undergo two to five generations (Bishop et al. 2001, Roberts, Umina, et al. 2011b). They survive the hot dry summer months by producing diapause eggs that are resistant to desiccation that hatch the following autumn in response to cooling temperatures and adequate rainfall (Wallace 1968, Roberts, Umina, et al. 2011b). This characteristic is thought to be important in *S. viridis* establishment in Australia since its introduction from Europe in the late 1800s (Wallace and Mahon 1971).

Sminthurus viridis have chewing mouthparts and feed by removing the leaf epidermis to reach the underlying mesophyll, leaving transparent patches of epidermis over the leaf surface. These patches can merge in severe infestations resulting in complete skeletonization of the leaf, followed by stunting and death of plant seedlings (Davidson 1934, Roberts et al. 2009). Control of *S. viridis* largely relies on the application of insecticides through foliar sprays or seed treatments (Micic et al. 2008, Roberts et al. 2009). Beyond chemicals, there are very few management options available for farmers in Australia, particularly at the vulnerable seedling stage. Several studies have found promising levels of control with two predatory mites, the pasture snout mite (*Bdellodes lapidara* Kramer [Acarina: Bdellidae]) and the spiny snout mite (*Neomolgus capillatus* Kramer [Acarina: Bdellidae]) in pastures in Western Australia and Tasmania (Wallace 1967, Ireson and Webb 1995, Ireson et al. 2002). Other studies, however, have failed to detect a beneficial impact of *B. lapidara* on *S. viridis* in different regions of Australia, questioning the broad-scale effectiveness of these biological control agents for *S. viridis* (Ireson 1984, Roberts, Weeks, et al. 2011c).

There are currently five chemical Mode of Action groups registered against *S. viridis* in Australia (APVMA 2020). Of these

five, three (pyrethroids, organophosphates, and neonicotinoids) are heavily used by Australian farmers (Umina, McDonald, et al. 2019b). Pyrethroids are ineffective against *S. viridis*, and rarely used against this pest, due to high inherent tolerance to this chemical group (Jones and Ferris 2000, Roberts et al. 2009). Organophosphates, such as omethoate, dimethoate, and chlorpyrifos, are the most commonly used insecticides to manage *S. viridis*. These are often applied prophylactically as a safeguard against infestations of this pest and other sympatric pest species, such as the red-legged earth mite, *Halotydeus destructor* Tucker (Prostigmata: Penthaleidae). Neonicotinoids are also widely used as a prophylactic treatment in crops vulnerable to early-season attack by *S. viridis* such as wheat, canola, barley, and oats. The use of imidacloprid, in particular, has increased substantially over the last decade in Australia (Umina, McDonald, et al. 2019b). Indeed, it is now difficult for Australian farmers to purchase canola without a neonicotinoid coating, with seed treatments also becoming commonplace in many cereals (Umina, McDonald, et al. 2019b). These practices, combined with the limited chemical rotational options available to farmers, are likely to create strong selection pressure for *S. viridis* to evolve resistance.

Globally, there are no documented cases of insecticide resistance in *S. viridis* (Mota-Sanchez and Wise 2020). Within Australia, however, farmers do appear to be experiencing increasing control difficulties in the field (Roberts et al. 2009; Cesar 2016, 2017), and this species is considered at high risk of evolving resistance (McDonald et al. 2019). Resistance to organophosphates and pyrethroids has recently been found in multiple populations of *H. destructor* in Australia after continuous exposure to these chemical groups (Umina et al. 2012, 2017; Maino et al. 2018). Despite these emerging concerns and the considerable selection pressure imposed on *S. viridis*, there have been no studies investigating insecticide sensitivity shifts in this species. Moreover, there is no established methodology to test the response of *S. viridis* to neonicotinoids despite the extensive use of this chemical group in Australia and elsewhere.

Here, we adapted a laboratory bioassay recently developed for *H. destructor* (Umina, Arthur, et al. 2019a) to assess the response of *S. viridis* to imidacloprid. We then collected and tested multiple field populations of *S. viridis* to examine responses against omethoate and imidacloprid. Sensitivity data was generated for both insecticides, which will be important for future monitoring of insecticide resistance in Australia.

Materials and Methods

Field Collections

Nine *S. viridis* field populations were collected from agricultural regions within Australia (Victoria, New South Wales, and Western Australia) between August and September 2018 (Table 1). Populations were collected from pasture and lucerne paddocks. One of these sites, Gannawarra, has no history of insecticide use for more than 10 yr, whereas the remaining sites have experienced frequent *S. viridis* infestations and have a long history of organophosphate use, in particular with omethoate. *Sminthurus viridis* were collected via suction using a Stihl SH55 blower vacuum with a fine gauze mesh placed over the end of the vacuum tube. Individuals were placed into plastic containers with paper toweling and vegetation and then transported back to the laboratory. Containers were stored at 4°C until *S. viridis* were required for testing (up to 3 d).

For each chemical, three individual bioassays were undertaken on different dates. *Sminthurus viridis* were collected from Gannawarra and included as a standard in all bioassays so that comparisons could be made across all populations tested.

Organophosphate Testing

The commonly used organophosphate insecticide, Le Mat (Cheminova, North Ryde, NSW, Australia), was used to generate sensitivity data and screen for signs of field resistance. Le Mat contains 290 g/liter of omethoate and the solution representing the recommended field rate for *S. viridis* was 290 mg a.i./liter of omethoate. Bioassays were performed following the methodology described in Roberts et al. (2009), but slightly adapted for plastic vials. Nine concentrations of omethoate ranging from 1×10^{-4} to 10 times the field rate, with the addition of the surfactant Tween at 0.01% (v/v) (Ecoteric 20; Thermo Fisher Scientific; Scoresby, Vic, Australia), were serially diluted and tested against each population. For each concentration, approximately 10 ml of solution was poured into a 15 ml plastic vial and swirled to ensure complete coating, with excess liquid discarded. Six to eight vials were coated for each concentration and were left to dry upside down on a drying rack overnight. The control vials were treated in the same manner, except water (with the addition of 0.01% Tween) was used. Eight *S. viridis* adults were then placed into each vial along with a leaf of common vetch (*Vicia sativa* L.), which provided food and humidity. Vials were sealed and placed in a controlled temperature cabinet at 18°C for 8 h. After this time, individuals were scored as alive (moving freely),

Table 1. Collection details of *Sminthurus viridis* field populations screened against omethoate and imidacloprid

Population	State	Latitude	Longitude	Date collected[a]
Gannawarra	VIC	–35.70	144.13	(1) 15 Aug 2018 (2) 20 Aug 2018 (3) 17 Sept 2018
Wanalta	VIC	–36.56	144.85	15 Aug 2018
Rushworth	VIC	–36.57	144.97	15 Aug 2018
Auchmore	VIC	–36.43	144.13	15 Aug 2018
Taminick	VIC	–36.34	146.13	19 Aug 2018
Brocklesby	NSW	–35.80	146.61	20 Aug 2018
Goombargana	NSW	–35.75	146.63	20 Aug 2018
Beaton	WA	–33.74	115.03	17 Sept 2018
Letchford	WA	–33.78	115.36	17 Sept 2018

VIC = Victoria, NSW = New South Wales, WA = Western Australia.

[a]Gannawarra was collected on multiple occasions and included in all bioassays.

incapacitated (inhibited movement), or dead (no movement over a 5 s period) (Roberts et al. 2009).

Neonicotinoid Testing

The bioassay used to test imidacloprid closely followed the methodology recently developed for *H. destructor.* This method uses a filter paper bioassay, which proved to be highly repeatable and was able to overcome several challenges of traditional assays when testing this mite species to imidacloprid (Umina, Arthur, et al. 2019a). Previous studies testing insecticide responses on *S. viridis* have used the same bioassay protocol developed for *H. destructor* (Roberts et al. 2009). A pilot study was undertaken to determine: 1) if this methodology was applicable to *S. viridis* and 2) the appropriate concentration range and exposure period. To do this, we exposed the Gannawarra population to eight concentrations of imidacloprid ranging from 1 to 6,000 mg a.i./liter and assessed *S. viridis* after 8, 24, 32, and 48 h using the approach described above. Clear concentration-mortality curves were generated at each exposure period (Supp Fig. S1 [online only]), with chi-square tests indicating logit models adequately fitted the data in all cases. Importantly, the control mortality was zero, across all scoring points. This pilot data demonstrated the suitability of the methodology for *S. viridis* and informed the experimental design we subsequently used.

To assess the response of imidacloprid against the nine *S. viridis* populations, serial dilutions of imidacloprid (100 g/liter) (Advantage; Bayer Australia, Hawthorn, Vic, Australia) were prepared with the addition of 1% (v/v) Tween. Eight concentrations of imidacloprid ranging from 1 to 1,000 mg a.i./liter, were tested against each population (Table 1). For each concentration, 50 µl of solution was placed in the center of a 3 × 3 cm square piece of filter paper that had been placed inside a 15 ml plastic vial. Six to eight replicates were prepared for each concentration. Eight *S. viridis* adults were immediately placed into each vial, which were then sealed. The control treatment was treated in the same manner, except water (with the addition of 1% (v/v) Tween) was used in place of the chemical. Vials were placed in a controlled temperature cabinet at 18°C. Individuals were scored as described above after 24 h.

Statistical Analysis

Incapacitated individuals invariably die and, therefore, do not contribute to the next generation. Because of this, incapacitated individuals were pooled with dead individuals for data analysis across all bioassays. Concentration-mortality curves were generated by plotting percentage mortality (mean with standard errors) against log chemical concentration. Mortality data was analyzed using a logistic regression model at each time point. Concentrations that resulted in 50% mortality (lethal concentration, LC) along with 95% CIs were estimated (Robertson and Preisler 1992, Venables and Ripley 2002). For each bioassay, any differences in population responses were assessed using a one-way analysis of variance (ANOVA) and then examined in pairwise comparisons using Tukey's Honest Significant Difference (HSD) method, which corrects for type I errors when performing multiple hypotheses tests (Hsu 1996). The interaction between population and concentration (differences in concentration-mortality slopes on the logit scale) was considered through a one-way ANOVA. Differences in slopes between populations were also compared using multiple pairwise comparisons adjusted with Tukey's HSD method.

For both insecticides, models accounting for chemical concentration and population provided a better fit compared with models accounting for only chemical concentration, as assessed by a large deviance between models and Akaike information criterion (AIC) values (imidacloprid: χ^2 = 125, df = 8, P < 0.0001, AIC difference = −110; omethoate: χ^2 = 132, df = 8, P < 0.0001, AIC difference = −117). Models accounting for concentration and population were used to compute regression slopes, LC_{50} values and the 95% CIs across all bioassays.

All analyses were conducted using R version 3.3.1 (R Core Team 2018).

Results

Omethoate

Control mortality was less than 10% across all bioassays. LC_{50} values for omethoate ranged from 1.65 (1.34–2.03) to 7.34 (5.96–9.03) mg a.i./liter, and regression coefficients from 0.905 (±0.073) to 2.962 (±0.453) (Table 2).

There was some variability among population responses to omethoate (Supp Fig. S2 [online only]), with significant pairwise differences between populations detected across all three bioassays (Table 2). In Bioassay 1, the Wanalta population had a higher LC_{50} value than the Auchmore population. In Bioassay 2, Brocklesby had a concentration-mortality curve shifted to the left of the other populations (Supp Fig. S2b [online only]), with this population exhibiting a lower LC_{50} value compared with all populations. Goombargana also had a lower LC_{50} value than Gannawarra and Taminick. In Bioassay 3, the concentration-mortality curve for Gannawarra was shifted to right of Beaton and Letchford (Supp Fig. S2c [online only]) and had a significantly higher LC_{50} value than *S. viridis* from Beaton (Table 2).

Differences in regressions slopes between populations were also observed in Bioassays 1 and 2. In Bioassay 1, the Wanalta population had a significantly steeper slope than all other populations, with Gannawarra also exhibiting a significantly steeper slope than Auchmore (Table 2). In Bioassay 2, the regression slope estimated for Taminick was significantly steeper than the slopes of Brocklesby and Goombargana (Table 2).

Imidacloprid

Control mortality was less than 5% across all imidacloprid bioassays. The LC_{50} values for imidacloprid ranged from 11.5 (9.23–14.33) to

Table 2. LC_{50} values (and 95% CIs) and regression coefficients (and standard error) for *Sminthurus viridis* populations when exposed to omethoate for 8 h

Bioassay no.	Population	LC_{50} (95% CIs) mg a.i./liter	Regression coefficient (b) ± SE
1	Gannawarra	4.16 (3.36–5.16)ab	1.519 ± 0.140b
	Wanalta	5.44 (4.60–6.43)a	2.363 ± 0.265a
	Rushworth	4.39 (2.83–6.81)ab	1.072 ± 0.157bc
	Auchmore	2.72 (2.07–3.59)b	0.905 ± 0.073c
2	Gannawarra	5.52 (4.52–6.75)a	1.892 ± 0.200ab
	Brocklesby	1.65 (1.34–2.03)c	1.563 ± 0.145b
	Goombargana	3.33 (2.67–4.14)b	1.396 ± 0.124b
	Taminick	6.19 (5.16–7.42)a	2.962 ± 0.453a
3	Gannawarra	7.34 (5.96–9.03)a	1.594 ± 0.151a
	Beaton	4.00 (3.33–4.81)b	1.903 ± 0.189a
	Letchford	5.51 (4.59–6.61)ab	1.800 ± 0.174a

Different letters within Bioassay No. represent significant differences (0.05 level, Tukey's HSD tests).

39.88 (32.85–48.42) mg a.i./liter, and regression coefficients from 1.108 (±0.088) to 2.114 (±0.213) (Table 3).

Responses to imidacloprid across the *S. viridis* populations varied (Supp Fig. S3 [online only]), with significant pairwise differences between populations detected in all bioassays (Table 3). In Bioassay 4, the Wanalta population had a significantly higher LC_{50} value than Rushworth. In Bioassay 5, Brocklesby and Taminick populations had concentration-mortality curves shifted slightly to the left of Gannawarra and Goombargana (Supp Fig. S3b [online only]); with these populations exhibiting higher LC_{50} values than both Brocklesby and Taminick (Table 3). In Bioassay 6, the concentration-mortality curve for Gannawarra was shifted to the right, with this population exhibiting a significantly higher LC_{50} value than the Beaton and Letchford populations (Supp Fig. S3c [online only]; Table 3).

Some differences in regression slopes between populations were observed after exposure to imidacloprid. In Bioassay 4, the Wanalta and Auchmore populations had significantly steeper slopes than the other two populations (Table 3). In Bioassay 6, the regression slope for Beaton was significantly steeper than the slopes estimated for Gannawarra and Letchford (Table 3).

Discussion

Research that establishes insecticide toxicity data for natural populations is important for monitoring insecticide responses in the future, particularly for species that have high exposure to chemicals in the field and/or are at high risk of evolving insecticide resistance (Umina, McDonald, et al. 2019b). This study generated important sensitivity data for the first time across multiple *S. viridis* populations from geographically distinct regions in Australia. The response of *S. viridis* to neonicotinoids was examined using a modified bioassay method recently developed for *H. destructor* to test imidacloprid (Umina, Arthur, et al. 2019a). We obtained concentration-mortality curves for *S. viridis* that were highly consistent across bioassays, demonstrating that this methodology is suitable for testing imidacloprid responses against this species. To our knowledge, this is the first time that responses to any neonicotinoid compound have been thoroughly tested on *S. viridis*, or indeed any other Collembolan species.

There were differences detected between field populations for both omethoate and imidacloprid, suggesting natural variation in how *S. viridis* responds to each of these chemicals. Importantly, however, there were no large discrepancies between population responses, with a maximum difference between LC_{50} values of ~3.7-fold (Taminick and Brocklesby after exposure to omethoate). Moreover, in no instance did any *S. viridis* individuals from any population survive at insecticide concentrations representing the field rate. This suggests insecticide resistance is not present in the field populations tested. In further support of this, *S. viridis* from Gannawarra tended to have the highest LC_{50} value to omethoate and imidacloprid, indicating it is one of the least sensitive populations. Yet this population has not been directly exposed to any insecticide for more than a decade, while the other populations have had repeated chemical exposure, particularly to omethoate. Additionally, the LC_{50} values established in this study for omethoate are comparable to, or lower than, the LC_{50} values generated for *S. viridis* over a decade ago (Roberts et al. 2009); there is no evidence to indicate a shift in omethoate sensitivity over that time, although the Roberts et al. (2009) study did only test a single field population, so any comparison is limited.

Table 3. LC_{50} values (and 95% CIs) and regression coefficients (and standard error) for *Sminthurus viridis* populations when exposed to imidacloprid for 24 h

Bioassay No.	Population	LC_{50} (95% CIs) mg a.i./liter	Regression coefficient (b) ± SE
4	Gannawarra	30.20 (24.42–37.33)ab	1.255 ± 0.103b
	Wanalta	37.33 (31.22–44.63)a	2.114 ± 0.213a
	Rushworth	21.81 (17.04–27.92)b	1.612 ± 0.165ab
	Auchmore	26.26 (21.74–31.72)ab	1.758 ± 0.146a
5	Gannawarra	28.54 (22.97–35.45)a	1.185 ± 0.097a
	Brocklesby	11.50 (9.23–14.33)b	1.266 ± 0.109a
	Goombargana	24.53 (20.19–29.81)a	1.544 ± 0.126a
	Taminick	15.20 (11.71–19.73)b	1.372 ± 0.140a
6	Gannawarra	39.88 (32.85–48.42)a	1.358 ± 0.115b
	Beaton	16.00 (13.35–19.18)b	1.921 ± 0.167a
	Letchford	17.39 (13.87–21.81)b	1.108 ± 0.088b

Different letters within Bioassay No. represent significant differences (0.05 level, Tukey's HSD tests).

Variation in insecticide susceptibility between field populations of conspecific species is not uncommon in baseline studies (Prabhaker et al. 2008, 2014; Clouston et al. 2016; Balanza et al. 2019; Umina, Arthur, et al. 2019a). Possible explanations include the age of individuals tested and environmental stressors such as temperature, humidity, and photoperiod, which can influence the physiological conditions of field-collected individuals used in bioassays (Omer et al. 1993, Prabhaker et al. 2008). Host plant differences can also impact the way in which herbivorous species respond to insecticides. Some plant types produce chemical compounds that are toxic to herbivores (Everist 1974, Kinghorn 1979, Dermauw et al. 2013). It is widely hypothesized that this leads to the selection of various detoxification mechanisms in species that feed upon these plants (Ambrose and Regupathy 1992, Umina et al. 2010, Dermauw et al. 2013). Genetic differences between populations may also contribute to variability in insecticide sensitivities (Prabhaker et al. 2008). In Australia, *S. viridis* have been found to have a strong population structure and relatively limited gene flow between regions (Roberts and Weeks 2011a), which may help to explain the results found in this study.

Of course, subtle population differences might also suggest that *S. viridis* is responding to local selection pressures imposed by repeated insecticide use. *Sminthurus viridis* from Wanalta had the highest LC_{50} values in Bioassays 1 and 4, and one of the highest LC_{50} values of all populations when every bioassay is considered. The Wanalta field has experienced extensive insecticide exposure in recent years and has, very recently, been found to contain *H. destructor* with low-level resistance to organophosphates (Arthur, unpublished data). Perhaps this *S. viridis* population is showing the first signs of chemical tolerance evolution (Clouston et al. 2016).

While no evidence of field resistance was detected in this study, *S. viridis* has recently been identified as a pest with a potentially high risk of evolving insecticide resistance. McDonald et al. (2019) estimated the resistance risk of ~80 Australian grain pests, including species that are known to have insecticide resistance. This analysis, which examined the evolutionary potential, off-target and targeted insecticide usage, and the availability of pest refuges, ranked *S. viridis* in the top five (ranked from highest resistance potential to lowest). So, why hasn't field resistance evolved in Australia? There are numerous factors that can impact a species' ability to evolve insecticide resistance, such as genetic predisposition, insecticide exposure, as well as behavioral and ecological factors (Roush and Mckenzie 1987). Resistance is expected to differ among arthropods depending on evolutionary constraints and rates of micro-evolutionary processes. For example, taxonomic groupings are expected to differ in the diversity in gene families

that are important in countering the effects of chemicals, particularly those gene families involved in detoxification (Rane et al. 2016). To date, there have been no reports of any collembola species evolving insecticide resistance (Mota-Sanchez and Wise 2020), which could point to the existence of genomic constraints within this subclass of arthropods. Alternatively, the lack of resistance might be linked to the polyphagous nature of *S. viridis* (Davidson 1934, Johnston 1960, Gu et al. 2007). This includes many host plants (including weeds and roadside vegetation) that are unlikely to be the target of chemical sprays, which in turn increases the proportion of individuals within a population that have no or very little exposure to chemicals. The wide range of unsprayed host plants attacked by *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) in North America has been assumed to be a key reason for the delayed evolution of resistance in this species despite the wide use of insecticides (McCaffery 1998).

In conclusion, this study established a reliable and robust bioassay methodology that enables the testing of the neonicotinoid, imidacloprid, against *S. viridis* under controlled laboratory conditions. This is crucial given the increased use of neonicotinoids over the last 10–20 yr in Australia and elsewhere. The sensitivity data generated for imidacloprid and omethoate provides a useful starting point for future resistance monitoring of this pest. Importantly, no evidence of resistance was detected in multiple field populations, despite the heavy reliance on chemicals to manage this pest and resistance being a widespread issue in many other important grain pests in Australia (Umina, McDonald, et al. 2019b) and elsewhere (Jensen 2000, Ahmad 2007, Furlong et al. 2013, Sparks and Nauen 2015). The occurrence of occasional long-distance dispersal events (Roberts, Umina, et al. 2011b) would aid the spread of resistance alleles if they were to arise in *S. viridis*. Australian farmers would be substantially impacted if resistance became widespread. The development of effective cultural and biological control options is needed.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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