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Ontogeny in the European earwig (Forficula auricularia) and grain crops interact to exacerbate feeding damage risk

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Abstract

The preference of herbivores for different host plants can be modulated by plant ontogeny. In agricultural pest management this has implications for sowing dates and pest monitoring. In the last 20 years, the European earwig (*Forficula auricularia*), a cosmopolitan pest, has been increasingly implicated in damage to grain crops in Australia. Among these, rape seed, *Brassica napus*, appears especially at risk, but little information on *F. auricularia* as a grain pest is available. We tested the susceptibility of seven grain crops commonly grown in Australia to infestation by *F. auricularia* using closed microcosm experiments, exposing plant seedlings at two early growth stages to four different life stages of *F. auricularia*. Lucerne and rape seed were shown to be the most vulnerable crops, and younger seedlings experienced significantly more damage than older seedlings across all crop types. Fourth instar *F. auricularia* were found to cause greater feeding damage than younger or older earwigs, while adults collected in winter generally caused more damage than those collected in summer. Surprisingly, even second instar *F. auricularia* caused greater damage than summer adults. This variation could reflect the ontogenetically dynamic nutritional needs of earwigs. Recent studies of *F. auricularia*'s life cycle in southern Australia indicate that these damaging life stages have some overlap with sowing dates of the crops tested here, exposing their vulnerable seedling stage to infestation. The phenology of *F. auricularia* in southern Australia therefore partly drives its ability to act as a pest. Future monitoring will likely need to track the distribution of *F. auricularia* life stages in order to effectively mitigate risks to vulnerable crops.

Keywords: grain pests, rape seed, lucerne, life stage, plant damage, pest management

Introduction

The European earwig, *Forficula auricularia* L. (Forficulidae: Dermaptera), is a cosmopolitan species (Lamb & Wellington, 1975) that has been repeatedly introduced outside of its native European range (Crumb, Eide & Bonn, 1941). *Forficula auricularia* is a social insect with an annual life cycle divided into two phases; the nesting phase and the foraging phase (Lamb & Wellington, 1975).

From mid- to late-autumn, adults mate aboveground and build shallow burrows to begin nesting (Crumb et al., 1941; Lamb & Wellington, 1975). In this phase, adults nest in the burrows during the day and emerge to forage at night (Lamb & Wellington, 1975). In winter, females oviposit in the nest and then chase the male out (Lamb, 1976). After eggs hatch, the female forages with the young and protects them for the first two instars (Lamb, 1976), although it does not seem that they are dependent on her for feeding (Meunier & Kölliker, 2012). In spring, third instars leave the nest permanently and begin the foraging phase. Some adult females may begin a second brood at this stage (Wirth, Le Guellec, Vancassel & Veuille, 1998) while the first broods go through their fourth instar and progressively emerge as adults in summer (Dib, Sauphanor & Capowiez, 2017; Lamb & Wellington, 1975; Tourneur, 2017). Under laboratory conditions, instars last roughly two weeks each (Crumb et al., 1941). This life cycle is mostly elucidated from studies of northern hemisphere populations, where *F. auricularia* is represented by a pair of cryptic sibling species which show high mitochondrial divergence, low reproductive compatibility, and slightly different life histories (Wirth et al., 1998).

The global distribution of *F. auricularia* has not been studied in detail, although it is generally considered an anthropophilic pest (Crumb et al., 1941). Records from the Global Biodiversity Information Facility show the highest density of reports in northern, western, and central Europe, southern Australia, New Zealand, the United States, and the Azores, with further isolated records from Morocco, the Canary Islands, central Mexico, northern Colombia and eastern Europe (GBIF, 2019). *Forficula auricularia* was introduced to Australia over 170 years ago (Quarrell et al., 2018). Only one of the two sibling species ('Clade B') is present in Australia and this is represented by fewer haplotypes than in Europe (Quarrell et al., 2018). *Forficula auricularia* has a broad distribution in Australia but appears mostly restricted to the southern states (Hill, Binns, Umina, Hoffmann & Macfadyen, 2018; Quarrell et al., 2018), likely because of its climatic envelope (Hill et al., 2018). Notably, *F. auricularia* in Australia is particularly associated with disturbed environments (Quarrell et al., 2018), in-line with its anthropophilic habits (Guillet, Guiller, Deunff & Vancassel, 2000; Lamb & Wellington, 1975). In Australia, depending on the geographic region, first instars typically begin emerging in mid-winter through early spring, third and fourth instars predominate by mid-spring, and by early summer, populations consist entirely of adults (Binns, Hoffmann, van Helden, Heddle & Umina, 2019; Quarrel, Corkrey & Allen, 2017).

The diet and foraging behaviour of *F. auricularia* as a predator is well-studied, especially in agricultural contexts where they are considered beneficial. The species is known to feed on several invertebrate pests, including aphids (Dib, Jamont, Sauphanor & Capowiez, 2011; Romeu-Dalmau, Espadaler & Pinol, 2012), midges (He, Wang & Xu, 2008), psyllids (Lenfant, Lyoussoufi, Chen, Faivre d'Arcier & Sauphanor, 1994), moth larvae (Nicholas, Spooner-Hart & Vickers, 2005) and earth mites (Weiss & McDonald, 1998). However, much of this research has been conducted in orchards (e.g. Suckling, Burnip, Hackett & Daly, 2006; Moerkens, Leirs, Peusens & Gobin, 2009; Logan, Maher & Rowe, 2017) and some studies have demonstrated interannual inconsistency in the species' ability to control invertebrate pests (Carroll & Hoyt, 1984; Carroll, Walker & Hoyt, 1985). Moreover, where *F. auricularia* effects control of one pest species, another co-occurring pest may be completely unaffected (Carroll & Hoyt, 1984). The functional role of *F. auricularia* in any one system is clearly complex and context-dependent. In grain systems, *F. auricularia* is regarded as a beneficial predator (Corpuz & Raymundo, 2010; Manyuli, Kyamanywa & Luther, 2008; Sunderland, Crook, Stacey & Fuller, 1987; Sunderland & Vickerman, 1980), except in Australia where it is widely considered a pest (Gu, Fitt & Baker, 2007; Murray, Clarke & Ronning, 2013; Micic et al., 2008).

Murray et al. (2013) recently assessed the risk posed by *F. auricularia* to Australian grain crops, and suggested that rape seed, *Brassica napus,* suffers greater economic damage compared with other crop types. At the time of the study*, F. auricularia* was estimated to cause AU $4.2 million in losses per annum in rape seed, with the potential for this to double in the absence of control measures. Moens & Glen (2002) list rape seed among the most vulnerable Australian grain crops due to its delicate cotyledon stage. Gu et al. (2007) also reported that seedling rape seed is the most common target of *F. auricularia* infestations. This is consistent with reports of field damage from southern Australian grain farmers which are disseminated through industry newsletters (Cesar, 2020). In cases where information on growth stage is provided, farmers most often report *F. auricularia* damage at the seedling stage or to crops with 2-4 true leaves (Cesar, 2020). Farmer field reports also detail damage to wheat, barley, lucerne (alfalfa), lupins, and pasture, but these are less frequent (Cesar, 2020). This species can also contaminate windrows at harvest time (Gu et al., 2007). Relatively few studies have quantified the susceptibility of plants to earwigs (Nicholas, Spooner-Hart & Vickers, 2004; Strauss et al., 2009) and it remains unclear what conditions induce populations of *F. auricularia* to become problematic in Australian grain systems.

Whether relative crop damage and the existing pattern of damage reports are matters of host preference in *F. auricularia* remains to be determined. Recently, Quintero & Bowers (2018) studied the interaction of plant and herbivore ontogeny in a specialist caterpillar, and their results highlight the need to consider the developmental stage of both organisms in order to predict plant damage. Combined knowledge of how plant development affects their vulnerability, and how *F. auricularia* differ in their feeding preferences and potential for feeding damage across its life cycle could allow crop damage to be better predicted and management strategies to be developed. The present study aimed to investigate the potential for feeding damage to a variety of grain crop seedlings by *F. auricularia*. Host plants at two different early growth stages were subjected to four different life stages of *F. auricularia*.

Materials and methods

The ability of *F. auricularia* at four different life stages to damage crop seedlings at two different growth stages was tested using closed microcosms in a controlled environment between July 2018 and June 2019. This method has been used previously to study invertebrate pest biology (e.g. Umina & Hoffmann, 2004; Douglas, Hoffmann, Umina & Macfayden, 2019). Second and fourth instars and adults were tested. Adults were examined at two different maturities; in December, recently post-imaginal moult, hereby referred to as summer adults, and in July, the second month of the species' nesting period in southern Australia (Binns et al., 2019), hereby referred to as winter adults. This was undertaken for two reasons. Firstly, it allowed us to better investigate the potential risk to grain crops sown at different times of the year. Secondly, food intake can depend on an insect's developmental state. For example, species can show different functional responses to the energetic demands of reproductive development (Strong, 1967; Hill, Luntz, & Steele, 1968). In *F. auricularia*, oogenesis is ongoing after adult emergence and continues well into the nesting phase (Tourneur, 1999), suggesting the possibility of seasonally dynamic feeding behaviours. Four identical experiments were conducted, with a different life stage of *F. auricularia* tested in each as they became available for collection.

Microcosms consisted of clear plastic cups (6.5 cm diameter base, 9 cm diameter top, 14 cm high) containing 5:1 sandy loam:potting mix. Crops and varieties assessed were lucerne (*Medicago sativa* cv. Sardi 7), rape seed (*B. napus* L. cv. Stingray), lupin (*Lupinus angustifolius* cv. PBA Jurien), red lentil (*Lens culinaris* cv. PBA Jumbo2), chickpea (*Cicer arietinum* cv. PBA Slasher (desi)), wheat (*Triticum aestivum* cv. Trojan), and oat (*Avena sativa* cv. Yallara). These were chosen because they are widely grown and among the most economically important grain crops in Australia.

For each crop, *F. auricularia* was introduced at two different stages of seedling development which were standardised across crop types using the BBCH scale (Hess et al., 1997; Lancashire et al., 1991) (Table 1). To synchronise crop seedlings with these growth stages for *F. auricularia* introduction, the sowing of seeds into microcosms was staggered over a 6-day period. Due to differences in size of the seedlings between crop types, plant numbers within microcosms were altered. For the first growth stage, four seedlings for all crops were established. For the second growth stage, four seedlings for lucerne and rape seed and three seedlings for lupin, lentil, chickpea, wheat, and oat were established. Following sowing, each microcosm was watered, enclosed with a clear plastic lid that had a gauze window for ventilation, and placed in a controlled temperature (CT) room maintained at 18±2°C and 60±10% RH under growth lights with a 12:12 L:D photoperiod. Microcosms were watered every 2-3 days as required throughout the experiment and humidity within each cup was maintained above 93% RH across all crop types and experiments. For each treatment, seven replicate cups were established. Earwigs were introduced to five microcosms, while two microcosms had no earwigs and acted as controls to ensure there was no plant damage due to other factors, and were used as plant references to compare against the damage caused by *F. auricularia* (see below).

Forficula auricularia specimens were collected prior to each experiment using traps made from rolled corrugated cardboard inside PVC piping which had been left for seven days in a field located in Elmore, Victoria (36° 28′59.43′′S, 144° 32′55.615′′E). Wheat was grown in this field in 2018 and rape seed in 2019, and no evidence of damage by *F. auricularia* was noted in either year. Prior to introduction into microcosms, *F. auricularia* were acclimated for 3-5 days at 4°C in sealed containers containing moist paper towel and a small amount of freeze-dried pollen for food. The first experiment used second instars, the second used fourth instars, and the final two experiments used adults. In each experiment, two randomly selected individuals were introduced into each microcosm. When adults were used, one male and one female were introduced; this was not possible for the earlier life stages as sexual dimorphism only becomes apparent in the adult stage.

Plant feeding damage was assessed at 1, 3, 7, and 14 days after introduction (DAI) of earwigs. Plant damage was assessed for each seedling individually by recording the proportion of plant matter damaged relative to that remaining, with results then averaged across seedlings within each microcosm. This was achieved by noting the total number of leaves and the surface area of leaves in the test plants, and visually comparing these with reference plants grown in the absence of *F. auricularia,* which represented ‘whole’ plants at each assessment timepoint. For example, when a rape seed seedling had four true leaves of equal size, each leaf was assigned a total proportion of 0.25. The proportion of missing tissue to each leaf was then estimated by comparing with the reference plants; these were then summed to determine the total damage to each plant. The number of living plants remaining within each microcosm was also recorded on each assessment day. Plants were determined to be killed (damage proportion of 1) when they had been completely defoliated or the stem was severed. Any dead earwigs were recorded and removed immediately to prevent cannibalism.

In order to investigate the potential impact of undertaking experiments in a controlled temperature (CT) room maintained at 18°C, an additional set of seven microcosms were established using rape seed at the first growth stage and were placed within a shade-house so that *F. auricularia* experienced climatic conditions representative of those in the field. These were included across all four experiments (i.e. covering each life stage of *F. auricularia*). Plant feeding damage, *F. auricularia* mortality and the total number of living plants were assessed as described above at 1, 3, 7, and 14 DAI.

Statistical analysis

We analysed the proportion of plant damage caused by *F. auricularia* using a beta regression model, which assumes the response variable to fall within a standard unit interval (0, 1) but can account for heteroscedasticity and skew (Ferrari & Cribari-Neto, 2004; Zeileis, Cribari-Neto, Grün & Kos-midis, 2010), which are common features of beta distributed variables. The proportion damage y_i of microcosm i is assumed to be a random draw from a Beta distributed random variable with mean μ_i and variance ϕ. Using a logit-link function, the mean μ_i is calculated from a linear predictor based on a matrix of covariates X and vector of unknown coefficients β.

$$y_i \sim \mathrm{Beta}(\mu_i, \phi)$$
$$\mathrm{logit}(\mu_i) = X^T\beta$$

Here, all covariates were categorical and included crop type, plant growth stage, and earwig life stage. Across all analyses, data at 14 DAI was used to ensure an independent data set avoiding pseudo-replication of repeated measurements through time. To test for the significance of treatment effects, likelihood ratio tests were performed on models that included and excluded the respective model term. To explore the effect of rearing conditions (CT room versus shade-house), the same analysis was performed on a subset of the data that only included CT and shade-house data collected for first growth stage rape seed. Shade-house data was excluded from all other analyses. Earwig mortality was analysed as above with the response variable (alive = 1, dead = 0) assumed to be a randomly distributed binomial variable. Due to low variability in mortality, data were pooled for juveniles (second and fourth instars) for model fitting. Analyses were conducted using R version 3.5.1 (R Core Team, 2019) and beta regression models were fitted using the *betareg* package (Zeileis et al., 2010).

Results

Forficula auricularia showed evidence of feeding on all crops tested, but there were considerable differences in the levels of damage caused between crop types ($\chi^2_6 = 274.5$, $p < 0.001$). The inclusion of crop type increased the explained variance in plant damage from 13% to 66%. The proportion of damage tended to plateau over the course of experiments, except for second instar *F. auricularia* which fed at a relatively consistent rate throughout the experiments (Figures 1 & 2).

Overall, lucerne experienced the highest level of feeding damage, followed by rape seed (Figures 1-3). Intermediate levels of feeding damage were observed to lupin and lentil seedlings, while wheat and oat seedlings suffered only minor feeding damage (Figures 1-3). Chickpea experienced the least amount of feeding damage, typically with only small chewing marks to a few leaves which remained consistent over time. At the second growth stage, lupin experienced comparable levels of feeding damage to rape seed and lucerne when exposed to both summer and winter adults (Figure 3).

The pattern of feeding damage when comparing crop types was generally consistent across plant growth stage and *F. auricularia* life stage. From most to least damaged crop, this was lucerne, rape seed, lupin, lentil, wheat, oat, and chickpea. Exceptions were chewing damage to chickpea stems at the first growth stage by fourth instar *F. auricularia* and winter adults, leading to higher overall mean plant damage than for oat and wheat (Figures 1-3). At the first growth stage, fourth instar *F. auricularia* also damaged lentil twice as much as lupin (Figure 3).

Crop seedlings at the first growth stage were more vulnerable to *F. auricularia* damage than those at the second growth stage ($\chi^2_1 = 36.5$, $p < 0.001$). The first growth stage was associated with approximately four times more damage than the second growth stage when comparing cases of non-zero damage across all time points, crop types and *F. auricularia* life stage. This' large impact of growth stage is evident in Figure 3. The use of three rather than four second growth stage seedlings for some crop types (i.e. lupin, lentil, chickpea, wheat and oat) did not appear to increase the relative damage scores in those microcosms by skewing the ratio of plant matter to earwig numbers.

All life stages of *F. auricularia* caused plant feeding damage, and these patterns were relatively consistent across the seven crop types examined. The different life stages were however associated with significantly different levels of feeding damage ($\chi^2_3 = 75.3$, $p < 0.001$), with the inclusion of life stage increasing the explained variance in feeding damage by 9% (Figures 1-3). Fourth instar *F. auricularia* were responsible for the greatest plant feeding damage, causing >10% damage to all crop seedlings at the first growth stage by 14 DAI (Figure 1). When we combined feeding scores across all crop types at the first growth stage, the mean damage observed at 14 DAI was 48%, 29%, 25%, and 22% for fourth instars, winter adults, second instars, and summer adults, respectively. When we did the same at the second growth stage, the mean damage at 14 DAI followed the same order by earwig life stage, with the greatest damage caused by fourth instars (30%) compared with winter adults (20%), second instars (12%) and summer adults (11%). While more damage was generally observed for winter adults compared with summer adults, this effect was not significantly different ($\chi^2_1 = 2.2$, $p = 0.14$) due to variance within treatments and the inconsistency of the pattern across all crop types (e.g. lentils and wheat experienced more damage from summer adults) (Figure 3).

In those microcosms where *F. auricularia* feeding resulted in plant death, more seedlings were killed at the first growth stage than the second growth stage (Table 2). The only exception to this was for lupin; no seedlings were killed at the first growth stage at 14 DAI, yet ~7% of lupin seedlings were killed at the second growth stage after feeding by fourth instar and winter adult earwigs (Table 2). Overall, lucerne and rape seed were found to be highly vulnerable to seedling mortality from *F. auricularia* feeding. Minor seedling loss was observed in chickpea and lupin microcosms, while no wheat, oat or lentil seedlings were killed by earwigs, regardless of plant growth stage or *F. auricularia* life stage (Table 2). There was no effect of treatment on mortality (crop type: $\chi^2_6 = 8.1$, $p = 0.23$; growth stage: $\chi^2_1 = 0.026$, $p = 0.87$), however there was a significant effect of life stage on *F. auricularia* mortality ($\chi^2_2 = 39.1$, $p < 0.001$). Mortality was low across all microcosms containing second instars (4%), fourth instars (zero) and summer adults (6%), however averaged 20% for the winter adults, presumably reflecting the end of their life-cycle.

There was no significant difference between the level of feeding damage caused by *F. auricularia* to rape seed when placed in a shade-house in ambient climatic conditions compared with CT conditions at 18°C ($\chi^2_1 = 0.43$, $p = 0.51$). For life stages collected in winter (second instars and winter adults) when the temperature difference between the two locations was greatest, individuals in the shade-house were slower to damage rape seed seedlings, but by 14-DAI had caused similar damage to those in the CT room (Suppl. Figure 1). Similarly, there was no difference in the total number of seedlings alive or the total number of surviving *F. auricularia* at 14 DAI between microcosms in the shade-house and those placed in a CT room; across all microcosms, there were 16 dead seedlings in both the CT room and shade-house, and there were four dead earwigs in the CT room and three dead in the shade-house. This suggests the feeding behaviour and mortality of *F. auricularia* was not greatly influenced by differences in temperature or rearing conditions.

Discussion

In this study we used controlled microcosm experiments to investigate the vulnerability of seven grain crops commonly grown in Australia to damage by the invasive European earwig, *F. auricularia*. The results demonstrate effects dependent on the life stage of both the host plant and insect. The different crop types also showed considerable variation in their susceptibility to damage by *F. auricularia*, although all experienced at least some level of feeding damage. Lucerne and rape seed were found to be particularly vulnerable, especially at cotyledon stage, which has important management implications for farmers where *F. auricularia* is known to be present.

Insect life stage effects

Second instars caused less damage than fourth instars, which is likely due to the difference in size between life stages. However, despite being larger, adult earwigs caused consistently less damage than fourth instars. This may reflect a physiological shift from somatic growth to somatic maintenance as *F. auricularia* move into their adult phase. While some insects undergo post-eclosion somatic growth, this is typically confined to the first two weeks immediately following eclosion (Norris, 1961; Strong, 1967; Walker, Hill & Bailey, 1970). The summer adults used in our experiments were collected in December, whereas *F. auricularia* adults typically emerge in November in southern Australia (Binns et al., 2019). If *F. auricularia* does indeed undergo post-eclosion somatic growth, it is likely that this had ceased prior to the collection and testing of the summer adults used in these experiments.

Likewise, the nutritional needs of adult *F. auricularia* may differ from those of juveniles and may further explain the differences in feeding patterns. For example, Unsicker, Oswald, Köhler & Weisser (2008) found ontogenetic changes in dietary preference in the grasshopper, *Chorthippus parallelus*, when presented with a mixture of plant foods, suggesting stage-specific nutritional requirements. They also found sex-specific effects, and there are reasons to suspect that female dietary preference would vary more so than male dietary preference in many insect species. Males may already contain sperm on eclosion as adults (Sehnal, 1985), but female insects have dynamic nutritional needs following eclosion that relate to reproduction. The oogenetic cycle in adult female *F. auricularia* is known to persist well into the nesting phase (Tourneur, 1999). This may explain, at least in part, why we found that summer adult *F. auricularia* generally resulted in less overall plant damage than their winter counterparts. Females collected during the nesting phase in winter may have had greater nutritional requirements than females collected in summer, which were unlikely to be nesting. However, since we did not separate adult individuals by sex, nor did we determine the oogenetic status of female earwigs, we could not directly examine whether these ontogenetic differences truly explain the differences in feeding levels.

Summer adults were collected from a wheat crop, while winter adults were collected from a field with rape seed. While no damage from *F. auricularia* was reported in either year, we cannot be certain that the earwigs had not fed on these plants prior to collection. It is well established that previous feeding experience by phytophagous insects can lead to a preference for this host in the future (e.g. Jermy, Hanson & Dethier, 1968; Cheng, Umina & Hoffmann, 2018). Damage to wheat was low by both adult maturities, though summer adults did consume slightly more leaf tissue than winter adults. Winter adults fed on rape seed more readily than summer adults, but this was also the case for lucerne and lupins, and by 14-DAI the level of damage to rape seed was the same for summer and winter adults. Therefore, any predisposition to the crops from which they were collected is unlikely to have significantly skewed our data.

Crop type and plant growth stage effects

Across crop types, younger seedlings at the cotyledon stage (or shortly after emergence for wheat and oat) were more vulnerable to *F. auricularia* damage than older seedlings with true leaves. Given the smaller size of the seedlings at the first growth stage compared with the second, the same amount of leaf tissue consumed would result in a greater proportion of damage in younger seedlings, which may go some way to explain this trend. Likewise, younger seedlings, particularly lucerne and rape seed, are less likely to survive *F. auricularia* feeding compared to seedlings with true leaves given younger seedlings are more readily defoliated and have reduced photosynthetic capacity. Younger seedlings are also likely to be more vulnerable due to the physical differences between plants at different growth stages (e.g. plant tissues being softer and easier to chew) (Hanley, Fenner & Edwards, 1995). The growth-differentiation balance hypothesis, whereby investment in plant defence is balanced against investment in tissue growth (Herms & Mattson, 1992) has also been used to explain why younger seedlings are generally more palatable to herbivores compared with more established plants. As the growth rate of plant tissue declines over the course of plant development, investment in plant defence (both physical and chemical) increases.

Variation in the physical architecture of crop seedlings is also likely to have influenced their relative susceptibility to attack from *F. auricularia*. For example, lucerne may be vulnerable to damage due to the slender nature of the seedling stems, while oat and wheat may be more tolerant due to the tough outer cuticle of the plant tissue (see Douglas, Macfadyen, Hoffmann & Umina, 2017). Although not examined in our study, differences in the timing of induced plant chemical defences could also explain some of the patterns observed in feeding damage between crop types. For example, chickpea was unpalatable to *F. auricularia* in our experiments, and where damage did occur (by winter adults to seedlings at the first growth stage), feeding declined thereafter. Pandey et al. (2017) found upregulation of transcripts involved in secondary metabolite production pathways within 20 minutes of mechanical wounding of chickpea leaves. In contrast, Vilariño, Mareggiani, Grass, Leicach & Ravetta (2005) found that lupin (*L. angustifolius* varieties) did not show an increase in alkaloid concentration in response to damage. Induced plant defence in response to herbivory is common (Karban & Baldwin, 2007) and has been observed in lucerne (Agrell, Oleszek, Stochmal, Olsen & Anderson, 2003), rape seed (Bodnaryk, 1992; Koritsas, Lewis & Fenwick, 1989, 1991), oat (Soriano, Asenstorfer, Schmidt & Riley, 2004), lupin (Chludil, Leicach, Corbino, Barriga & Vilariño, 2013), chickpea (Pandey et al., 2017; Singh, Singh & Verma, 2008) and wheat (Piesik et al., 2010). However, generalists, such as *F. auricularia*, tend to be less sensitive to plant secondary metabolites than specialist herbivores (Sorensen, McLister & Dearing, 2005), which vary in their deterrent effect on generalists (Macel et al., 2005) so effects would be crop-specific.

<u>Feeding patterns and crop risk</u>

Across hemispheres, first generation fourth instar earwigs emerge in spring (Binns et al., 2019; Orpet, Crowder & Jones, 2019), allowing an energetically demanding life stage to coincide with the period of highest primary productivity. Our results suggest that juveniles are capable of causing considerable damage; as much or even more so than adult *F. auricularia*. The early instars can feed independently (Meunier & Kölliker, 2012), and have been observed foraging independently in rape seed fields in Australia. Only field trials can confirm which of *F. auricularia*'s life stages are of most concern to farmers, but the present results suggest monitoring should make note of the ratio of instars present over the course of an infestation. In southern Australia, second instars are most common in July, and fourth instars are most common from September to October but begin emerging in August (Binns et al., 2019). This is much later than the common sowing dates for rape seed (late April through May), offering some temporal protection of seedlings against juveniles, although some varieties may be sown as late as August (Grains Research and Development Corporation, 2019). Earlier-sown varieties will still come into contact with winter adults and early instars, risking considerable damage. Behaviourally, early instars tend to be found on the ground (Beall, 1932), while fourth instars and adults are more likely to climb up plant structures (Tourneur, 2017). While we have demonstrated second instars have the potential to cause significant damage to young seedlings, it may be the case that early instars rarely encounter crops in the field when seedlings are small enough to be consumed without climbing, making them less of a threat to crops such as lucerne and rape seed.

Lucerne is generally grown year-round and thus faces the greatest exposure to *F. auricularia*. This, coupled with the consistently high damage sustained across plant growth stages and *F. auricularia* instars, suggests that lucerne is at considerable risk of damage in the field. Despite this, there appear to be relatively few field reports of *F. auricularia* damaging lucerne in Australia (Cesar, 2020). The reasons for this remain unclear, although it may, at least in part, reflect a reporting bias. Farmers may not report, or even monitor, lucerne damage by *F. auricularia*, as earwigs are not a previously recorded pest of this crop in Australia (Bailey & Goodyear, 2007; Umina, 2019). Within Australia, lucerne is often sown to manage salinity and groundwater recharge in areas which are otherwise dominated by annual grain crops (Angus, Gault, Peoples, Stapper & Van Herwaarden, 2001; Fedorenko, Dolling, Loo, Bailey & Latta, 2009). Lucerne is also widely used because it provides nitrogen inputs for grain crops grown in subsequent years (Hirth, Haines, Ridley & Wilson, 2001). Our results suggest that the strategic use of lucerne in southern Australia may be hindered by the presence of *F. auricularia*.

Conclusions

Our results provide empirical support to the growing evidence of the risk to grain crops posed by the invasive *F. auricularia*. Within Australia, rape seed has been particularly targeted by *F. auricularia*, and this appears to be caused by the plant’s high susceptibility, which has recently been found against other facultative herbivorous arthropods such the pillbug, *Armadillidium vulgare*, and the millipede, *Ommatoiulus moreletii* (Douglas et al., 2017; Umina, 2019). Other grain crops appear to have less associated risk, but there is still potential for *F. auricularia* infestations to damage lupin and lentil crops. While few Australian farmers have thus far reported earwig damage to lucerne, this crop is clearly at high risk considering its perennial nature and high susceptibility to *F. auricularia* feeding. Monitoring of *F. auricularia* infestations should ideally take into account the insect's life cycle when assessing crop risk, especially as this pertains to sowing dates for winter grains. Our findings demonstrate that seedling crops face potential defoliation in cases of high-density infestations of *F. auricularia*.

Conflict of Interest Statement

The authors declare no conflicts of interest.

Author contribution

P.A.U. conceived the ideas and designed the methodology alongside L.S.K.; L.S.K conducted the experiments; J.M. conducted the statistical analyses and prepared the figures; O.S. and L.S.K. led the writing of the manuscript, with input from P.A.U. P.A.U. secured funding. All authors read and approved the manuscript.

Data availability statement

Data will be archived in the DRYAD public repository upon manuscript acceptance.

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Figure legends

Figure 1. Cumulative mean plant feeding damage (%) over time for each crop type at the 1st growth stage. Five replicate microcosms were assessed for each crop, containing 3-4 seedlings and two *F. auricularia* individuals. Error bars represent standard errors of the mean.

Figure 2. Cumulative mean plant feeding damage (%) over time for each crop type at the 2nd growth stage. Five replicate microcosms were assessed for each crop, containing 3-4 seedlings and two *F. auricularia* individuals. Error bars represent standard errors of the mean.

Figure 3. Mean plant feeding damage (%) for each crop type subsetted to show data at 14 days after *F. auricularia* introduction to (A) 1st growth stage and (B) 2nd growth stage plants. Five replicate microcosms were assessed for each crop, containing 3-4 seedlings and two *F. auricularia* individuals. Error bars represent standard error of the mean.

Supplementary Figure 1. Boxplots showing mean plant feeding damage (%) to rape seed seedlings at the 1st growth stage when located in a CT room at 18°C (grey bars) and a shade-house (white bars). Five replicate microcosms were assessed for each crop, containing 3-4 seedlings and two *F. auricularia* individuals.

Table 1. Crop type and growth stages at the time of *F. auricularia* introductions.

Crop	**Plant growth stage**	
	First	Second
Lucerne	D9 - unfolding cotyledons	D12/13 - two or three leaves
Rape seed	D9 - unfolding cotyledons	D12/13 - two or three leaves
Lupin	D9 - unfolding cotyledons	D14 - four trifoliate leaves
Lentil	D9 - shoot through the soil surface	D17 - seven multifoliate leaves
Chickpea	D9 - shoot through the soil surface	D17 - seven multifoliate leaves
Wheat	G10 - first leaf through coleoptile	G13 - three leaves
Oat	G10 - first leaf through coleoptile	G13 - three leaves

Plant growth stages are defined according to the BBCH scale (Lancashire et al., 1991; Hess et al., 1997).

Table 2. Mean percentage of seedlings killed for seven grain crops at two growth stages by *F. auricularia* at different life stages 14 days after introduction into microcosms. Five replicate microcosms were assessed for each crop, containing 3-4 seedlings and two *F. auricularia* individuals.

Crop	***F. auricularia* life stage**															
	2nd instar				**4th instar**				**Adult (summer)**				**Adult (winter)**			
	Plant growth stage				Plant growth stage				Plant growth stage				Plant growth stage			
	1st		2nd		1st		2nd		1st		2nd		1st		2nd	
	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
Lucerne	30	18.4	0	0	100	0	65	18.7	30	9.4	0	0	50	11.2	10	10
Rape seed	0	0	0	0	55	20	5	5	10	6.1	0	0	5	5	0	0
Lupin	0	0	0	0	0	0	6.6	6.6	0	0	0	0	0	0	6.7	6.7
Lentil	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Wheat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chickpea	0	0	0	0	1	6.1	0	0	0	0	0	0	10	6.1	0	0

s.e. represents stand error of the mean.

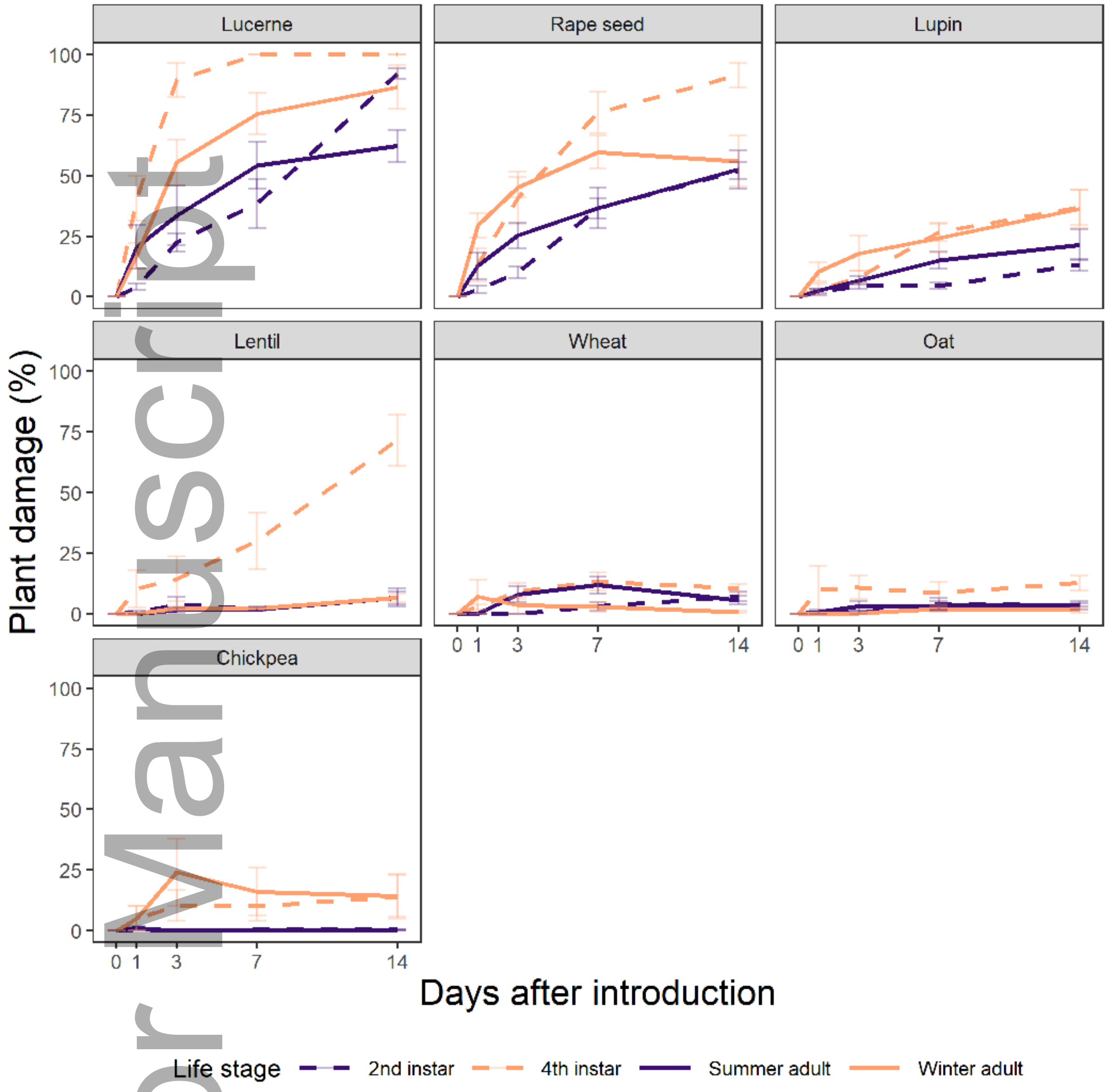

Figure 1. Cumulative mean plant feeding damage (%) over time for each crop type at the 1st growth stage. Five replicate microcosms were assessed for each crop, containing 3-4 seedlings and two *F. auricularia* individuals. Error bars represent standard errors of the mean.

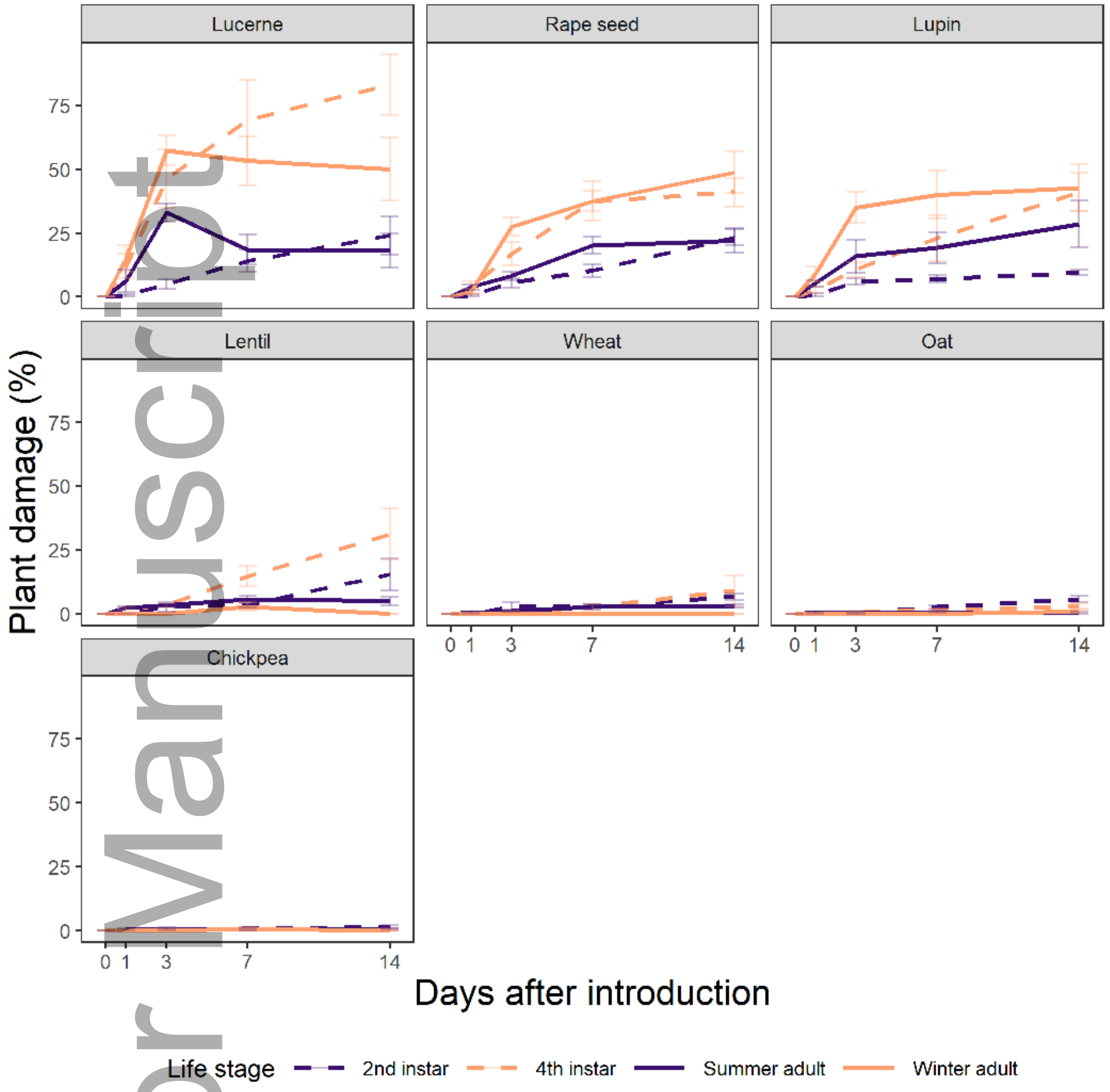

Figure 2. Cumulative mean plant feeding damage (%) over time for each crop type at the 2nd growth stage. Five replicate microcosms were assessed for each crop, containing 3-4 seedlings and two *F. auricularia* individuals. Error bars represent standard errors of the mean.

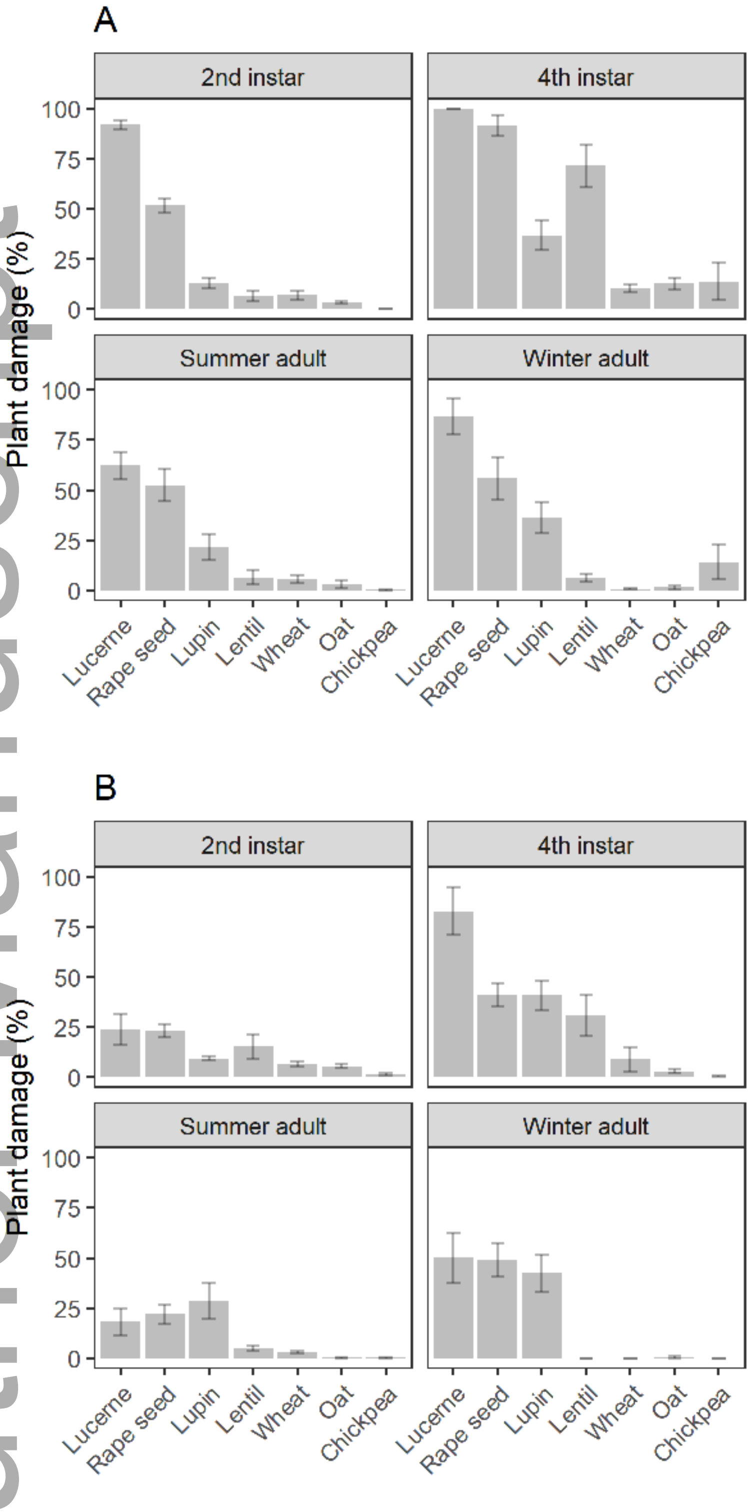

Figure 3. Mean plant feeding damage (%) for each crop type, subsetted to show data at 14 days after *F. auricularia* introduction to (A) 1st growth stage and (B) 2nd growth stage plants. Five replicate microcosms were assessed for each crop, containing 3-4 seedlings and two *F. auricularia* individuals. Error bars represent standard error of the mean.