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Oviposition and larval establishment of three 'generalist' noctuids on *Capsicum annuum*

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Abstract

Understanding the oviposition and foraging behaviour of pestiferous lepidopterans on their economically important food plants guides the development of effective pest management tactics. Here, we examined the oviposition behaviour and larval establishment of three noctuid species on a single crop—capsicum (*Capsicum annuum*). We selected pest species that are known to infest capsicum crops to varying degrees—the cotton bollworm, *Helicoverpa armigera*; the cluster caterpillar, *Spodoptera litura*; and the fall armyworm, *Spodoptera frugiperda*. Although related, these species differ in their known host-plant preferences and larval feeding behaviour. We conducted a series of glasshouse experiments examining moth oviposition and larval survival on different crop stages and the ability of neonate larvae to feed and establish on capsicum fruits at different stages of development. Although all three species oviposited on capsicum plants, *S. litura* laid more eggs than the other species and targeted most of their eggs to plants rather than the cage wall, indicating a preference for the plant. *S. litura* larvae demonstrated the highest level of survival (48%) when left unrestricted on capsicum plants, whereas only a small proportion of *S. frugiperda* (12%) and *H. armigera* (3%) larvae survived on capsicum plants. Surprisingly, most surviving *S. frugiperda* larvae were found feeding inside capsicum fruits. The results generated in this study demonstrate how in-field infestations of these noctuids in capsicum arise and will guide further development of pest management strategies for these pests in capsicum.

KEYWORDS
bell pepper, foraging behaviour, integrated pest management, Noctuidae, preference-performance hypothesis, sweet pepper

INTRODUCTION

The oviposition and foraging behaviour of lepidopteran pests on their economically important food plants have received considerable research attention. Understanding moth and caterpillar behaviour underlies the development of sampling strategies, economic thresholds, biological control and host-plant resistance. There are a plethora of studies examining single pest species on multiple crop species or varieties to determine how herbivores are impacted by plant traits (e.g., defences) (Mitchell et al. 2016; Sharma, Sujana, & Manohar Rao 2009) or to examine the host range of a pest species of interest (Volp, Zalucki, & Furlong 2022). Yet there are surprisingly few studies examining and documenting differences among several pest species inhabiting and feeding on the same crop (Hoy & Shelton 1987; Liu, Scheirs, & Heckel 2012; Sokame et al. 2020).

This current study focuses on the economically important horticultural crop capsicum (*Capsicum annuum*; also known as bell pepper or sweet pepper) and three of its Lepidopteran pest species (Table 1)—*Helicoverpa armigera* (Hübner), *Spodoptera litura* (Fabricius) and *Spodoptera frugiperda* (J. E. Smith). All three species belong to the family Noctuidae and are major agricultural pests, known for their broad host ranges and their evolved resistance to many chemical insecticides which make them difficult to manage (Bragard et al. 2019; Downes et al. 2017; Montezano et al. 2018; Van den Berg & du Plessis 2022; Walsh

TABLE 1 Characteristics of three noctuid pest species examined in this study.

Species	Pest status in capsicum	Distribution	Reported host range	Feeding ecology
Helicoverpa armigera	Major	Australasia, Asia, Europe, Africa and South America	Wide—monocots and dicots	Adult and larval preference for flowering and fruiting crop stages but larvae can feed on leaves.
Spodoptera litura	Major	Australasia and Asia	Wide—preference for dicots	Highly preferential leaf feeder but larvae can feed on flowers/fruits.
Spodoptera frugiperda	Reported but uncertain	Australasia, Asia, Africa and Americas	Wide—preference for monocots	Preference for vegetative stage C4 grasses. Typically, a leaf feeder but larvae have been recorded feeding on reproductive plant parts (e.g., inside corn cobs, on sorghum heads).

et al. 2022). Their geographical distributions differ, but since the global spread of *S. frugiperda*, all three species now occur in the Asia-Pacific region (Bragard et al. 2019; Downes et al. 2017; Maino et al. 2021).

Although these pest species have been labelled as 'generalists', they differ in important aspects of their host range, ecology and feeding behaviour (Table 1). *H. armigera* is highly polyphagous and typically infests and feeds on plants during their flowering and fruiting crop stages, where larvae can cause significant yield penalties (Liu, Scheirs, & Heckel 2010; Volp, Zalucki, & Furlong 2024a; Zalucki et al. 1986). *S. litura* has a wide reported host range, but the pest favours dicots where it typically causes defoliation, although it has been recorded feeding on fruiting structures (Bragard et al. 2019). Finally, *S. frugiperda* also has a long list of reputed hosts, but the true host range of this pest is contentious due to two 'strains' of *S. frugiperda* which reportedly differ in their host-plant preferences (Durand, An, & Nam 2024; Nagoshi & Meagher 2022). However, in the invasive range of *S. frugiperda*, the pest displays a clear preference for warm season cereals, particularly *Zea mays* (Montezano et al. 2018; Volp, Zalucki, & Furlong 2022). Larvae of *S. frugiperda* typically infest cereals during their vegetative stages and feed on leaves inside the plant whorl, but they can also infest cobs (Morrill & Greene 1973; Pannuti et al. 2016). We hypothesised that these distinct dissimilarities in host range and feeding behaviour would result in marked differences in how capsicum plants are infested by these pest species.

All three species have been reported as infesting and attacking capsicum crops to varying degrees (Bragard et al. 2019; Jeger et al. 2017; Kay 2007). *H. armigera* is considered a significant pest of the crop due to the pest's preference for feeding on capsicum flowers and fruits (Kay 2007). *S. litura* is also regarded as an important insect pest of capsicum, although it primarily causes damage by leaf feeding (Bragard et al. 2019; Nagal, Verma, & Rathore 2016). Both pests are long-term capsicum pests for the Asia-Pacific region, where they regularly require insecticide intervention for control (Kay 2007; Nagal, Verma, & Rathore 2016). Often, crops are prophylactically sprayed with insecticides to control these pests due to consumer preferences for 'high-quality' fruit with limited defects (Ekman, Goldwater, & Winley 2016).

The status of *S. frugiperda* as a pest in capsicum is less certain than the other two species. Although capsicum is reported as a host-plant of *S. frugiperda* (Montezano et al. 2018), the pest does not have a reputation as a major pest of the crop and has demonstrated poor performance on capsicum in experimental evaluations (Tanaka, Mizutani, & Murata 2024; Wu et al. 2021). However, interception data indicates that almost half (21/46) of reported detections of *S. frugiperda* entering Europe in fresh produce between 1995 and 2017 were larvae found in capsicum fruits (Jeger et al. 2017). Similarly, since *S. frugiperda* was reported from Australia in 2020, there have been reports of larvae being detected in capsicum fruits during post-harvest packing (Subramaniam 2022). A preliminary survey of capsicum crops in Northern Queensland, Australia, detected *S. frugiperda* at a frequency of 0% to 16% of plants sampled (mean = 4%, $n = 10$ crops) and an infestation of 35% of fruits infested was recorded from a capsicum processing facility (Subramaniam 2022). These observations have prompted a more detailed investigation into the interactions between *S. frugiperda* and capsicum plants and in particular a comparison with the other two known pests to help guide the development of effective sampling and management strategies.

The aim of this study was to examine oviposition behaviour, larval establishment and foraging behaviour to understand infestation patterns of the three noctuid pest species on whole capsicum plants. We aimed to examine differences among the three pest species while investigating the following: (i) moth oviposition on reproductive stage capsicum plants, (ii) neonate larval survival and performance on capsicum plants at different reproductive stages and (iii) the ability of neonate larvae to feed on capsicum fruits of different development stages.

MATERIAL AND METHODS

Plants

Capsicum (cv. Warlock) seeds (sourced from Withcott Seedlings) were germinated in 24 cell (100-mL capacity

per cell) seedling trays in plant growth rooms (12:12 photoperiod, 25°C) where they were grown under artificial lights (Mars Hydro™) in a commercial potting mix (Searles Premium™). Seedlings emerged in 1–2 weeks and were watered as required. After 9 weeks, capsicum plants were transplanted into 4-L plastic ANOVA™ pots filled with potting mix (Searles Premium™) and transferred into a temperature-controlled glasshouse (27°C day, 25°C night) located at the Queensland Department of Primary Industries (QDPI) facility in Toowoomba, Queensland (−27.534994, 151.930483). In the glasshouse, plants were grown under natural photoperiod and irrigated via a drip system twice daily for 5 min. All three experiments were conducted in the same glasshouse facility.

To minimise the risk of sunburn to capsicum fruits, the western side of the glasshouse roof was covered by shade cloth, which reduced photosynthetically active radiation by approximately 60%. To ensure fruit development and prevent blossom end rot, beginning at 17 weeks post sowing, plants were fertilised weekly with a 150-mL water solution containing potassium sulphate (K 41.5%, S 17%) (Richgrow™) equivalent to 0.375 g per pot and calcium nitrate (N 15.5%, Ca 19.3%) (National Plant Supplies™) equivalent to 0.0075 g per pot, which replicated in-field fertiliser application rates.

Capsicum plants were regularly visually inspected for the presence of pests which were either physically removed or managed by releasing predatory insects—*Typhlodromips montdorensis* Schicha (Acari: Phytoseiidae) for thrips control and *Harmonia conformis* Boisduval (Coleoptera: Coccinellidae) for aphid control, both purchased from a local supplier of biocontrol agents (Bugs for Bugs™). Inundative releases occurred once for each natural enemy, and no natural enemies (or glasshouse pests) were present on plants when experiments were conducted. No chemical insecticides were applied to plants used in experiments.

Flower buds were manually removed from plants until 11 weeks post sowing. Bud removal prevented fruits from forming on small plants and ensured synchronous flowering and fruit development on experimental plants. Under these growing conditions, budding commenced shortly after bud removal ceased at 11 weeks, flowers emerged at 13 weeks, small green fruit appeared at 14 weeks and soon began expanding and fruits began to turn red approximately 21 weeks after sowing.

Insects

Insects were sourced from laboratory cultures maintained at the QDPI laboratory in Toowoomba. The source material for *S. frugiperda* was collected from maize and sweetcorn crops from South-East Queensland, *H. armigera* was derived from larvae collected from South-East Queensland crops and supplemented by material from a NSW Department of Primary Industries laboratory culture and the *S. litura* colony originated from collections from crops in the Ord Irrigation Area, Western Australia. All three pest species had been kept in culture for several generations, but field-collected insects were incorporated semi-annually in an attempt to minimise inbreeding depression.

The moth cultures were maintained on soybean flour-based artificial diet and reared using methods described elsewhere (Volp, Zalucki, & Furlong 2022, 2023). Briefly, moths were kept in 5-L plastic buckets and supplied with 10% sucrose solution for nutrition. Nappy liner (bamboo rayon) was secured over the top of buckets and used as an oviposition substrate. Eggs were removed regularly, and upon hatching, neonate larvae were placed in plastic containers (17.5 cm × 12 cm × 6 cm) with artificial diet; see Volp, Zalucki, & Furlong (2023) for ingredients. Upon reaching third/fourth instar, larvae were transferred into 32-well plastic trays with fresh diet, where they remained until pupation. Pupae were washed in 1% sodium hypochlorite solution and then placed on paper towel in plastic containers (17.5 cm × 12 cm × 6 cm) within mesh cages (60 cm × 60 cm × 60 cm, polyester mesh, Bugdorm™) until moth emergence, whereupon they were supplied with 10% sucrose solution. Moths were allowed several days to mate in the emergence cages before they were transferred into buckets for oviposition. The *H. armigera* and *S. frugiperda* cultures were kept in a temperature-controlled room at 25°C. To prevent prolonged larval development and to synchronise the availability of adults/eggs for experiments, the *S. litura* were kept in a temperature-controlled room at 28°C. Both rooms had a 12:12 photoperiod and were maintained at 60% relative humidity.

Experiment 1—Oviposition choice

For the oviposition choice experiment we sourced pupae from the respective laboratory colonies. Pupae were separated by sex with examination under a stereomicroscope (Nikon™, SMZ800N). We placed male and female pupae of each species into individual emergence cages (24 cm × 24 cm × 24 cm, BugDorm™) which were checked daily and upon emergence moths were removed and immediately paired and used in oviposition assays (i.e. no moths selected for assays were older than 24 h post eclosion).

For oviposition assays, groups of six moths per species (3♀:3♂) were placed into polyester mesh cages (68.5 × 68.5 × 121.9 cm, Nasco™) in the glasshouse. In the test cages, moths were provided with 10% sucrose solution as a carbohydrate source from a wicking container. Within each cage, we placed three capsicum plants, one of each crop stage—flowering (buds, flowers and small green fruits present), mid-fruiting (only green fruits present) and late fruiting (mostly red fruits present). At the commencement of assays, flowering plants were

between 95 and 102 days after sowing (DAS), mid-fruiting 123–130 DAS and late fruiting 158–165 DAS. We allowed moths four nights to feed, mate and lay eggs. Soil-filled pots were placed underneath shorter plants to account for differences in plant height among the crop stages and ensure plant canopies were at the same height.

After four nights we terminated assays and recorded the number and the location of egg masses and eggs on plants and cage walls. This methodology has been successfully used for examining moth oviposition behaviour in both *H. armigera* and *S. frugiperda* (Volp, Zalucki, & Furlong 2022, 2023). We also recorded the height of capsicum plants, counted the number of leaves and reproductive structures and took three measurements with an atLEAF™ meter on three separate young fully expanded leaves from the top of the plants. atLEAF™ meters have a leaf clip sensor which measures radiation absorbance to determine chlorophyll content, which is used as a proxy for leaf nitrogen content (Padilla et al. 2018). The experiment was a randomised block design, with 10 replicates for each moth species.

Experiment 2—Larval survival and performance on whole plants (10 days)

For the second experiment, we examined larval performance on capsicum plants of the same three crop stages used in Experiment 1 (flowering, mid-fruiting and late fruiting). Capsicum plants were placed in the same type of cages used in Experiment 1, with only one crop stage × pest species combination per cage. On each plant, we placed 50 neonate larvae (<24 h old) on a fully expanded leaf at the top of the plant. We left larvae unrestricted on the plants for 10 days, after which we destructively sampled plants and searched for larvae. Our searching of plants occurred shortly after sunrise and finished mid-morning. We recorded the number of surviving larvae, their location and instar. This experiment was a randomised block design, and four replicates were conducted for each crop stage × pest species combination.

Experiment 3—Neonates on caged fruits (4 days)

In the final experiment we caged neonate larvae of the three noctuid species on capsicum fruits at one of four fruit development stages: (1) small green fruit (recently formed and expanding fruit <40-mm diameter), (2) green fruit (nearly fully expanded), (3) turning fruit (in the process of changing colour from green to red) and (4) red fruit (full-sized fruits fully red in colour).

Ten neonate larvae of a single species were placed onto each fruit and restricted with the use of 13 × 12 cm organza mesh bags which were securely tied around the peduncle of each fruit. After 4 days, bags were removed and fruits destructively examined for the presence of larvae. We recorded the number of surviving larvae, their location and the presence of feeding damage on the fruits. We measured capsicum fruit wall toughness using a fruit penetrometer (FT-011, TR Turoni™), and we recorded a proxy for soluble sugars by taking Brix measurements of the fruit wall with a refractometer (PAL-1, Atago™). This experiment was a randomised block design, and four replicates were conducted for each fruit stage × pest species combination.

Statistical analysis

For the moth oviposition experiment, we analysed response variables using one-way or two-way ANOVAs where relevant with replicate used as a blocking factor. For both larval experiments we analysed larval response variables and relevant fruit variables using two-way ANOVAs with moth species and crop/fruit stage as the independent variables. For larval location data in the second experiment, we separated the three species and conducted one-way ANOVAs. Residual plots were checked for all analyses to ensure assumptions were met. All analyses were conducted using R version 4.4.2 (R Core Team 2019). Post hoc comparisons were made with Fisher's protected LSD test using the R package 'agricolae' (De Mendiburu 2020), and figures were made with the R package 'ggplot2' (Wickham 2016).

RESULTS

Experiment 1: Moth oviposition choice

Moths of all three species laid eggs in all cages except for a single *H. armigera* replicate where not a single egg was found. As this cage was an outlier (other *H. armigera* replicates contained between 86 and 818 eggs), we removed it from the analysis. Although both *Spodoptera* species in our experiment lay their eggs in masses, we analysed and presented data in terms of total egg counts for ease of comparison among the three species.

Moth species differed in the total number of eggs laid per cage in the oviposition assay ($F = 149.9$, $df = 2, 17$, $P < 0.001$; Figure 1). *S. litura* moths laid significantly more eggs than the other two species (Figure 1). Moth species also differed in the proportion of eggs they laid on plants compared with non-plant surfaces ($F = 21.73$, $df = 2, 17$, $P < 0.001$; Figure 2). Both *S. litura* (99.5%) and *H. armigera* (74%) laid most of their eggs on plants, whereas *S. frugiperda* only laid 32% of their eggs on plants, with the remainder laid on the cage wall and occasionally wicking containers. In terms of total number of eggs oviposited onto plants, there was a difference among species ($F = 170.21$, $df = 2, 17$, $P < 0.001$) with *S. litura* laying more than the other two species.

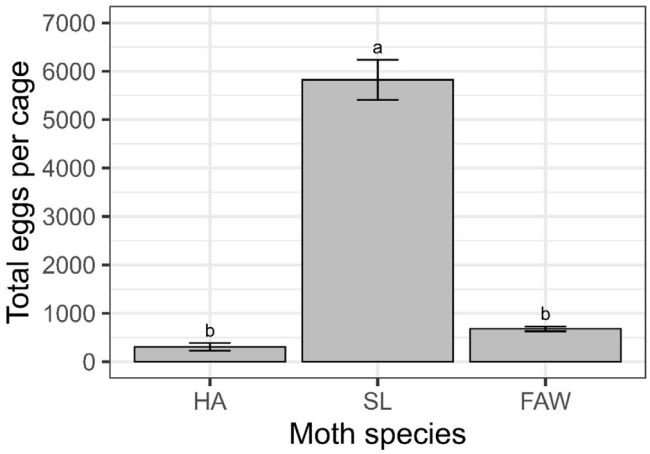

FIGURE 1 The average number of total eggs laid per cage (on plants and other surfaces) by moths during the oviposition choice assay. Bars represent the means and error bars represent standard errors. Letters above bars indicate a significant difference according to Fisher's protected LSD test. FAW, *Spodoptera frugiperda*; HA, *Helicoverpa armigera*; SL, *Spodoptera litura*.

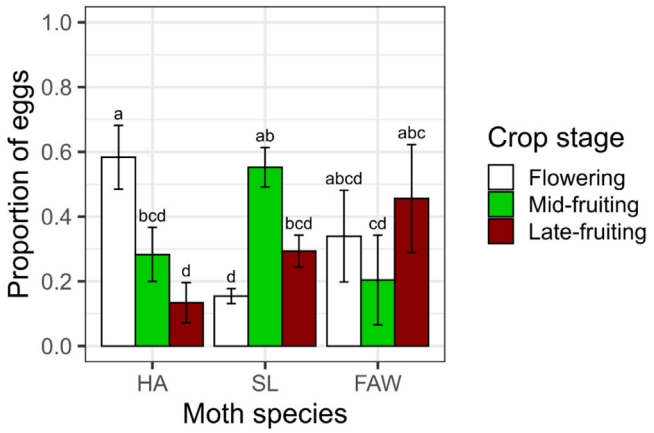

FIGURE 3 The proportion of eggs laid onto capsicum plants of different crop stages during the oviposition choice assay. Bars represent the means and error bars represent standard errors. Letters above bars indicate a significant difference according to Fisher's protected LSD test of the crop stage × moth species interaction effect. FAW, *Spodoptera frugiperda*; HA, *Helicoverpa armigera*; SL, *Spodoptera litura*.

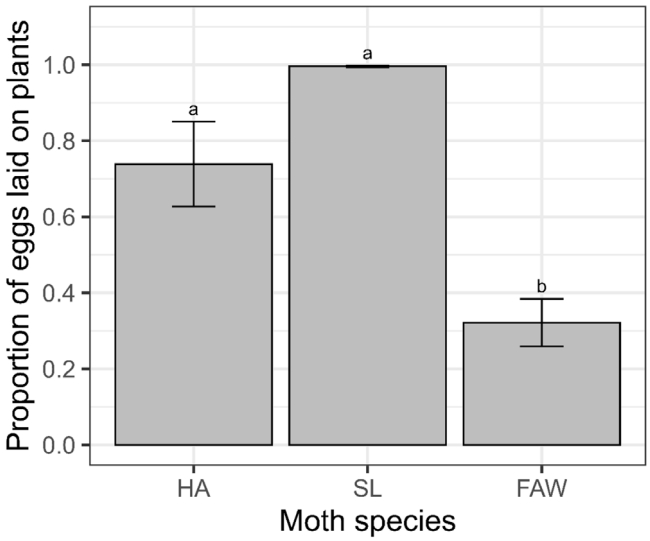

FIGURE 2 The proportion of eggs per cage which were laid on capsicum plants (as opposed to other surfaces—the cage wall and adult diet wick containers) by moths during oviposition choice assay. Bars represent the means and error bars represent standard errors. Letters above bars indicate a significant difference according to Fisher's protected LSD test. FAW, *Spodoptera frugiperda*; HA, *Helicoverpa armigera*; SL, *Spodoptera litura*.

Of the eggs laid on plants, we examined if the moth species preferred different plant growth stages (Figure 3). Replicates were removed where no eggs were laid on plants ($n = 1$ from *H. armigera* and $n = 2$ from *S. frugiperda*). A two-way ANOVA showed no difference among crop stages ($F = 0.45$, df = 2, 63, $P = 0.64$) or moth species ($F = 0$, df = 2, 63, $P = 1$), but there was a significant moth species × crop stage interaction ($F = 5.23$, df = 4, 63, $P < 0.01$). *H. armigera* preferred to lay eggs on flowering plants and *S. litura* preferred to lay eggs on plants at the mid-fruiting stage, followed by the late fruiting stage. *S. frugiperda* did not show a preference for crop stage. The choice experimental design prevented analysis of egg location data on different crop stages, but we note that for all species, regardless of crop stage, most eggs laid on plants (>75%) were laid on leaves.

In the oviposition experiment, plants varied in several traits depending on crop stages (Table 2). Flowering plants were shorter than the fruiting crop stages ($F = 20.74$, df = 2, 72, $P < 0.001$) and stem diameter increased with plant age ($F = 48.69$, df = 2, 72, $P < 0.001$). The atLEAF measurements indicated leaf nitrogen was highest during the mid-fruiting stage followed by flowering and then late-fruiting plants ($F = 37.53$, df = 2, 72, $P < 0.001$). Fruiting stage plants had more leaves than the flowering plants ($F = 19.17$, df = 2, 72, $P < 0.001$). None of the measured plant traits differed significantly among moth species.

We did not conduct ANOVA analysis on reproductive structures because of the absence of structures in some crop stages (Table 2). Both buds and flowers were only present on flowering stage plants. Green fruits were mostly present on flowering and mid-fruiting stage plants, although they differed in size (Figure S1). On the flowering plants, 95% of the fruit were below 20 mm in diameter, whereas fruits on the mid-fruiting plants were mostly above 20 mm (Figure S1). Few (6/30) late-fruiting stage plants had any green fruits present. Turning fruit and red fruits were only present on late-fruiting stage plants.

TABLE 2 Plant morphometric data from the oviposition choice experiment.

Crop stage	N	Plant height (mm)	Stem diameter (mm)	atLEAF measurement	Mean count per plant					
					Leaves	Buds	Flowers	Green fruits	Turning fruits	Red fruits
Flowering	30	444 ± 10.3 b	9.1 ± 0.18 c	53.5 ± 0.78 b	57.6 ± 2.26 b	9.6 ± 0.81	4.7 ± 0.41	8.1 ± 0.49	-	-
Mid-fruiting	30	516 ± 9.2 a	10.9 ± 0.23 b	57.5 ± 0.83 a	79.5 ± 3.36 a	-	-	7.1 ± 0.41	-	-
Late fruiting	30	515 ± 10.2 a	11.7 ± 0.18 a	47.5 ± 0.96 c	74.3 ± 3.11 a	-	-	0.2 ± 0.09	0.5 ± 0.16	7.8 ± 0.41

Note: Plants grown in the glasshouse were randomly allocated to moth species treatments; therefore, data are not separated by species. Values represent means ± standard errors for all the plants used for the respective crop stage. Lettering indicates a significant difference ($P < 0.05$) according to fisher's protected least significant difference test among crop stages. Relevant results from ANOVAs are presented in the text. '-' indicates that the respective plant structures were absent from that crop stage.

TABLE 3 Two-way ANOVA results for the 10-day larval survival experiment. Values in bold indicate a significant difference ($P < 0.05$).

Factor	df	*F* value	*P* value
Moth species	2	71.37	**<0.001**
Crop stage	2	8.42	**<0.01**
Species × crop stage	4	3.73	**0.017**
Block (replicate)	3	0.33	0.80

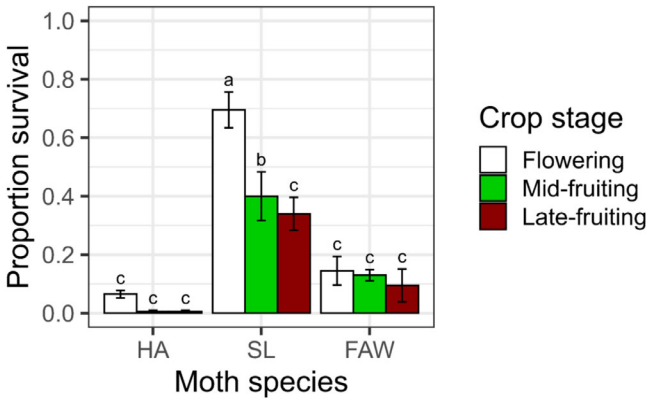

FIGURE 4 Larval survival on plants 10 days post placement of $n = 50$ neonates. Bars represent the means and error bars represent standard errors. Letters above bars indicate a significant difference according to Fisher's protected LSD test of the crop stage × moth species interaction effect. FAW, *Spodoptera frugiperda*; HA, *Helicoverpa armigera*; SL, *Spodoptera litura*.

Experiment 2: Larval establishment and survival on whole plants

In the unrestricted larval establishment experiment, we were able to relocate 378 of the 1800 neonate larvae placed on plants. Two were cadavers (both *S. frugiperda*) and the remaining were alive. Most of the recovered live larvae were from the *S. litura* treatment (where 287 survived from the 600 initially placed), followed by *S. frugiperda* (74/600), and then *H. armigera* (15/600). Larval survival was significantly influenced by moth species and crop stage, and there was a significant interaction effect (Table 3 and Figure 4). Ten days after neonate placement, most larvae from all three species had developed to third instar or later (Figure S2).

We were interested in understanding where larvae were located at the end of the assay to provide some information on feeding site preference. To analyse the location selection of larvae, we separated the moth species and the crop stage treatments (because the crop stages differ in the availability of sites to larvae). We did not analyse the locations of the *H. armigera* larvae because the mid- and late-fruiting treatments both only had a single replicate consisting of a single surviving larva. Although the flowering stage treatment had surviving larvae across four replicates, they were in low numbers (13 larvae across the four replicates). On the flowering plants, most *H. armigera* larvae (10/13) were found at fruits, with two larvae on the cage wall and a single larva on a leaf.

For *S. litura*, at the end of the 10-day experiment, larvae demonstrated a strong preference for leaves. Larvae were predominantly found at leaves in all three crop stages—flowering ($F = 14.74$, df = 4, 12, $P < 0.001$), mid-fruiting ($F = 21.79$, df = 3, 9, $P < 0.001$) and late fruiting ($F = 131.7$, df = 3, 9, $P < 0.001$; Figure 5).

For *S. frugiperda* at flowering we removed one replicate due to only a single larva surviving. At flowering, *S. frugiperda* larvae were randomly distributed among plant locations ($F = 0.99$, df = 4, 8, $P = 0.46$; Figure 6). Whereas during the mid-fruiting stage, most *S. frugiperda* larvae were located on or in the fruits ($F = 28.4$, df = 3, 9, $P < 0.001$). Of the larvae located at fruits, 15/20 were located inside green fruits. We excluded the late-fruiting crop stage from analysis because only two replicates had surviving larvae ($n = 19$ larvae total); 17/19 of these larvae were found at red fruits (15 of which were inside the fruits). The two dead *S. frugiperda* cadavers located in this experiment were also found inside a red fruit.

Experiment 3: Neonates on caged fruits

At the end of the caged fruit assay, there was no difference among moth species in their survival on capsicum fruits ($F = 1.70$, df = 2, 33, $P = 0.20$) nor was there an effect of fruit stage on larval survival ($F = 1.30$, df = 3, 33, $P = 0.29$; Figure 7). Of the 480 larvae (of all three

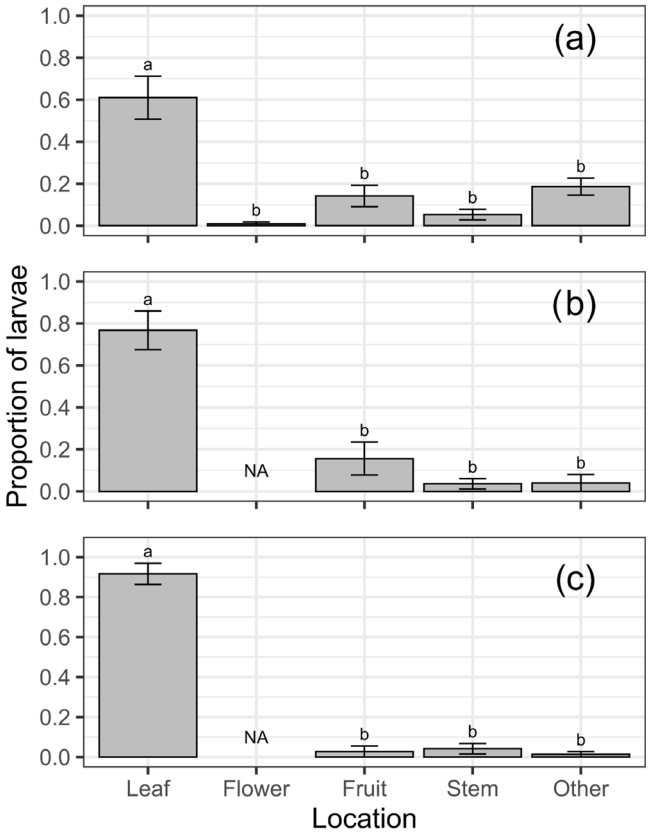

FIGURE 5 Distribution of *Spodoptera litura* larvae on plants after 10 days on the three separate crop stages: (a) flowering, (b) mid-fruiting and (c) late fruiting. Note that flowers are not present on mid- and late-fruiting stage plants. 'Other' includes on the soil surface, the pots and the cage. Bars represent the means and error bars represent standard errors. Letters above bars indicate a significant difference according to Fisher's protected LSD test among plant locations within a crop stage.

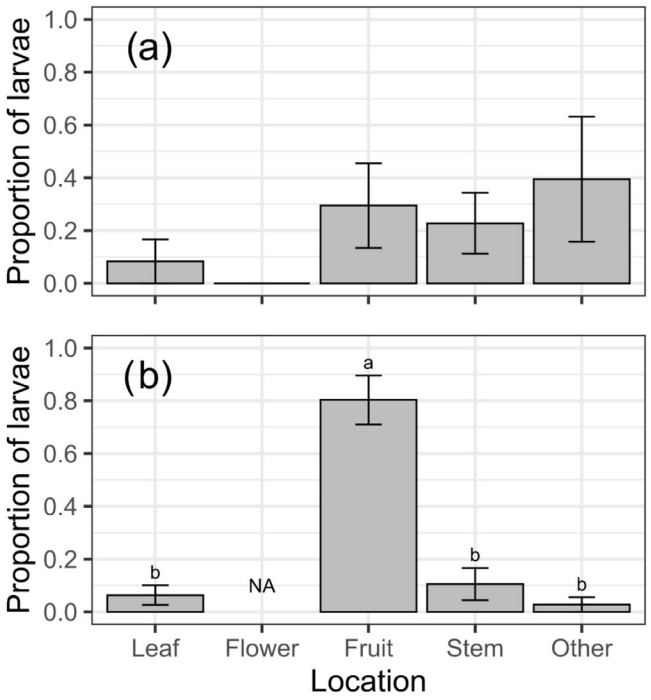

FIGURE 6 Distribution of *Spodoptera frugiperda* larvae on plants after 10 days on (a) flowering and (b) mid-fruiting plants. The late-fruiting stage was removed due to insufficient replication. Note that flowers are not present on mid-fruiting stage plants. 'Other' includes on the soil surface, the pots and the cage. Bars represent the means and error bars represent standard errors. Letters above bars indicate a significant difference according to Fisher's protected LSD test among plant locations within a crop stage.

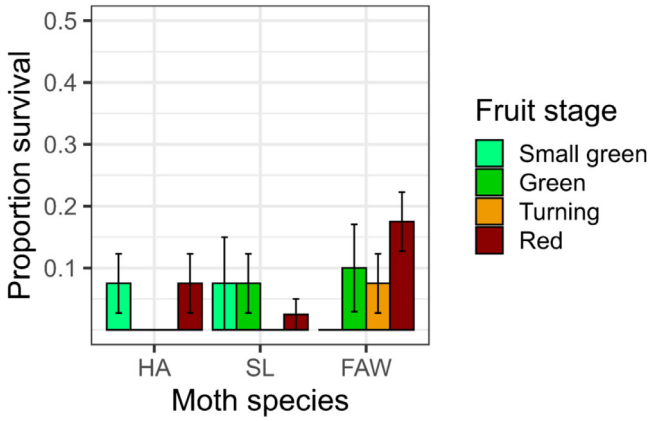

FIGURE 7 Larval survival in the caged fruit experiment. Bars represent the means and error bars represent standard errors. FAW, *Spodoptera frugiperda*; HA, *Helicoverpa armigera*; SL, *Spodoptera litura*.

species) placed on fruits in the experiment, we were only able to relocate 27 live larvae (14 *S. frugiperda*, 7 *S. litura* and 6 *H. armigera*) after 4 days. Of these larvae, most (18/27) were located feeding under the fruit's calyx (Figure S3)—a feeding behaviour that occurred in all three species. Only two larvae had made their way to feed inside the fruits—both were *S. frugiperda*, one in a green fruit and another in a turning fruit. Both of the penetrating larvae had tunnelled into the fruit through the bottom of the fruit at the apex rather than through the fruit wall underneath the calyx.

We detected several differences among fruit stages based on the physiochemical measurements we recorded during the caged fruit experiment. Fruit stages differed in their width ($F = 51.20$, df $= 3, 33$, $P < 0.001$; Figure 8a), with red fruit being the largest and small green fruit the smallest. Fruit stages also differed in the amount of force required to penetrate the fruit wall with a penetrometer ($F = 20.17$, df $= 3, 33$, $P < 0.001$; Figure 8b). Finally, the stages differed in the level of soluble sugars present in the fruit wall as detected by Brix measurements ($F = 61.30$, df $= 3, 33$, $P < 0.001$; Figure 8c).

DISCUSSION

In this study we conducted a series of glasshouse experiments to examine the relationships between the horticultural crop capsicum and three of its lepidopteran pests (*H. armigera*, *S. litura* and *S. frugiperda*). We conducted

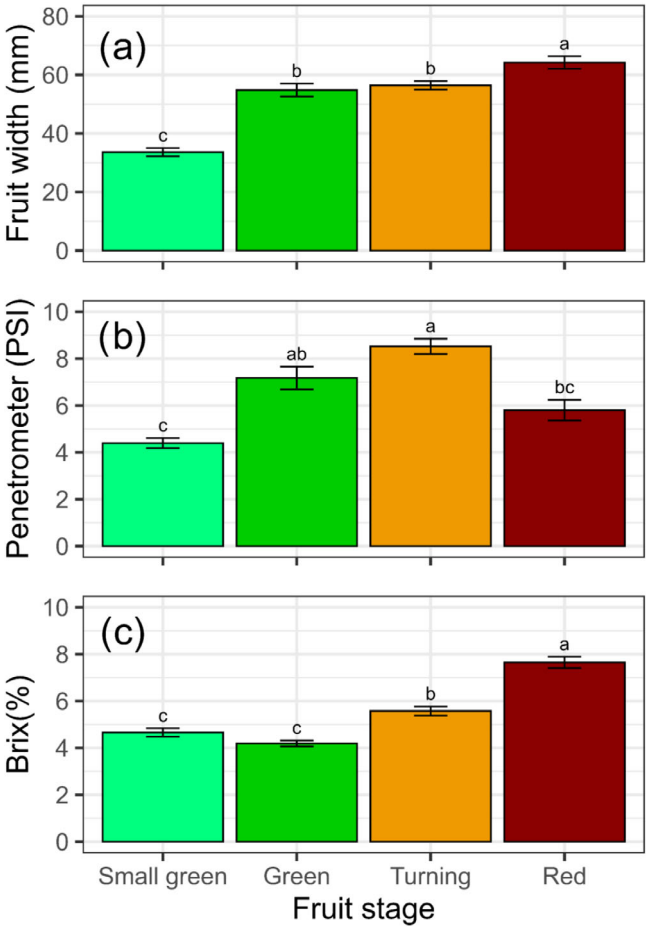

FIGURE 8 Fruit variables recorded the caged fruit experiment: (a) fruit width, (b) fruit wall toughness represented by penetrometer measurements of PSI (pounds per square inch) and (c) soluble sugar measurements as represented as brix measurements (%). Bars represent the means and error bars represent standard errors. Letters above bars indicate a significant difference according to Fisher's protected LSD test.

three experiments, first examining moth oviposition onto capsicum plants at reproductive crop stages (flowering, mid-fruiting and late fruiting). We then examined the survival of unrestricted larvae on the three crop stages. And finally, we investigated the ability of neonates to survive on capsicum fruits of different stages under no-choice conditions. Our results demonstrate that all three species oviposit on capsicum plants, but they differ drastically in their likelihood to do so. Similarly, we found that larvae of all three species can survive on capsicum plants, including when neonates are restricted to feeding only on fruits. But the way in which and level at which the species survive on capsicum plants dramatically differs.

In the oviposition experiment, *S. litura* laid many more eggs than the other two species (Figure 1). The vast majority of *S. litura* eggs were placed on plants, as were the majority of *H. armigera* eggs, whereas *S. frugiperda* placed most of its eggs on non-plant surfaces (Figure 2). These results yield several significant insights. Firstly, *S. litura* had a much greater reproductive output than the other two species across the experimental period (4 days post eclosion). We regularly observed egg masses in *S. litura* cages after the second night of the assay, whereas we did not observe eggs laid from *H. armigera* and *S. frugiperda* within two nights post eclosion. A shorter pre-ovipositional period combined with the larger size of *S. litura* moths may provide this species with a reproductive advantage over the other two species.

The second key piece of information from the oviposition assay was the non-preference of *S. frugiperda* towards capsicum plants. High levels of oviposition onto experimental cages are a regular feature of oviposition assays involving this species (Guo et al. 2021; Sotelo-Cardona et al. 2021; Volp, Zalucki, & Furlong 2022). However, when a preferred host is present (e.g., *Z. mays*), moths will apportion a similar number of eggs to plants and cages (Guo et al. 2021; Sotelo-Cardona et al. 2021; Volp, Zalucki, & Furlong 2022). Therefore, the low level of oviposition onto plants in the current experiment indicates that capsicum is not a preferred plant species for *S. frugiperda* moths, aligning with *S. frugiperda*'s documented preference for C4 cereal crops (Montezano et al. 2018).

Both *H. armigera* and *S. litura* displayed preferences for certain crop stages (Figure 3). It is unsurprising that *H. armigera* preferred to lay eggs on the flowering crop stage as this species has a well-documented preference for flowering plants (Liu, Scheirs, & Heckel 2010; Volp, Zalucki, & Furlong 2024a). What was more intriguing was the preference of *S. litura* for plants of the mid-fruiting crop stage. This preference may be explained by the large number of leaves (typical oviposition sites for *S. litura*) and high atLEAF measurements (a proxy for leaf nitrogen) of plant leaves at the mid-fruiting stage (Table 2).

In the 10-day unrestricted larval experiment we found differences in survival among species and crop stages (Table 3 and Figure 4). The least surprising result from this experiment was the high survival of *S. litura* on capsicum plants, given the moth's demonstrated preference for capsicum plants in the first experiment. We also recorded that most *S. litura* larvae were located on leaves (Figure 5), which aligns with the species' reputation as a leaf feeder. Interestingly though, larval survival was greatest on flowering stage plants rather than the mid-fruiting stage plants—even though mid-fruiting plants were the preferred crop stage of ovipositing moths (with the most leaves and highest atLEAF values). This result contradicts the oft-cited preference-performance hypothesis, which posits ovipositing mothers should select plants or sites superior for their offspring (Gripenberg et al. 2010; Mayhew 2001). Several potential explanations may account for this result. Perhaps larval populations establish better on the younger leaves of flowering capsicum plants compared with the older leaves of later stage plants. Alternatively, *C. annuum* cultivars have secondary metabolites which can affect *S. litura* performance (Vijaya & Rani 2017; Yuan et al. 2022) and varying concentrations of these

defensive chemicals among crop stages may also influence the preference-performance disconnect for *S. litura* observed in our study.

Larval survival of *H. armigera* was surprisingly low in the 10-day unrestricted larval experiment (Figure 4), especially given this pest's status as the major lepidopteran pest of capsicum in Australia (Kay 2007). We are not certain why the survivorship we recorded was so low and how this aligns with *H. armigera* population dynamics in capsicum crops in the field. A potential explanation for our results is that highly susceptible *H. armigera* neonates are dependent on floral sites like buds and flowers for establishment (Volp, Zalucki, & Furlong 2024b). But individual capsicum plants do not have many of these structures (Table 2) in comparison with highly suitable *H. armigera* hosts like pigeonpea (Volp, Zalucki, & Furlong 2023). Therefore, the carrying capacity of a capsicum plant may be much lower than other hosts and consequently *H. armigera* larvae may suffer very high mortality from lack of suitable feeding sites for neonates on capsicum plants.

Despite *S. frugiperda* moths largely avoiding ovipositing on capsicum plants, a surprising proportion of larvae were able to feed and survive. The ability of *S. frugiperda* to feed, survive and develop through to pupation on plant species that moths do not prefer has been demonstrated previously (Volp, Zalucki, & Furlong 2022). At the flowering stage, *S. frugiperda* larvae were distributed randomly among the plant locations, but at the mid-fruiting stage, larvae that survived were mostly inside fruiting structures (Figure 6). This result aligns with the observations from capsicum packing facilities in Australia and pest interception data from Europe (Jeger et al. 2017; Subramaniam 2022).

On a preferred host like *Z. mays*, *S. frugiperda* larvae will predominantly feed within enclosed plant structures like inside the plant's whorl on vegetative plants or inside cobs on reproductive stage plants (Morrill & Greene 1973; Pannuti et al. 2016). On non-preferred broadleaf crops (where there are no whorls present), larvae appear to feed at other plant locations where they can be concealed or partially concealed. This behaviour was demonstrated by larvae selecting to feed in fruits or under calyces in our larval experiments. Another example of this behaviour is in cotton crops, whereby *S. frugiperda* larvae have been recorded feeding at the junction between plant stem and petiole (Singh et al. 2023). It appears that thigmotaxis is highly important in the selection of feeding sites for this species and *S. frugiperda* larvae are 'partially concealed feeders'. Understanding the mechanisms that drive feeding location in *S. frugiperda* requires further research in preferred and non-preferred plant species. However, any such future experiments should consider whether larvae move to different feeding locations as a function of the day–night cycle, as we have observed *Spodoptera* spp. larvae changing their behaviour and location between night and day (T. Volp. pers. obs.).

In the final experiment, despite there being significant differences among the fruit stages in terms of size, wall toughness and sugar content (Figure 8), there was no difference in larval survival among the fruit stages. There was also no difference in survival among the three lepidopteran species when placed on fruits, despite the difference in feeding site preferences recorded in the earlier experiment. Prior to this final experiment, we expected that as capsicum fruits ripen and soften, larvae may find the process of mechanically penetrating the fruit with their mandibles easier. Although red fruit was softer and had a higher soluble sugar concentration than green and turning fruit, there were no differences in larval penetration or survival.

When drawing conclusions from the caged fruit experiment, one must consider the no-choice set-up of this assay; as neonates did not have an opportunity to select other sites to feed or shelter. For instance, under a free choice scenario, *S. litura* would have likely dispersed from the fruits and selected to feed at leaves instead, where larvae would have likely experienced much higher rates of survival (e.g., mean *S. litura* larval survival was 48% in the second [unrestricted] experiment after 10 days, compared with 4% larval survival in the caged fruit experiment after 4 days). Similarly, *S. frugiperda* and *H. armigera* larvae may have also preferred to feed elsewhere. It is worth noting, however, that the high levels of early instar larval mortality seen in Experiment 3 (and Experiment 2 to a lesser extent) are not unusual; it has been well documented that neonate caterpillars experience very high levels of mortality on their foodplants (Kyi, Zalucki, & Titmarsh 1991; Zalucki, Clarke, & Malcolm 2002).

We intentionally investigated neonates during the caged fruit experiment to examine if first instars could make their way into fruits, building upon our observations in the second experiment of limited damage to other plant parts from *S. frugiperda* (indicating very small larvae can fruit feed). It is important to note that larval feeding ability can change drastically as larvae age and the mandibles of first instars are likely not to be adapted to chewing into fruiting structures (Johnson & Zalucki 2007; Suits, Reisig, & Burrack 2017; Volp, Zalucki, & Furlong 2024b). Regardless, the caged fruit experiment was useful in documenting that (i) small larvae of all three species can feed and survive on capsicum fruits, at least for a short period, and (ii) the preferred feeding sites of larvae on capsicum fruits are at the top of the fruit underneath the calyx or on the bottom of the fruit (near the apex). These data provide an indication as to how larvae (particularly *S. frugiperda*) find their way inside capsicum fruits.

Regarding management implications for the three species in capsicum, firstly, although *S. litura* demonstrated the largest fecundity and strongest preference for capsicum plants, the species should be the easiest to manage in-field due to its exposed feeding habit. From our results, we can infer that *S. litura* would likely also be a problem during vegetative crop stages. Given the long crop

duration of capsicum, we suspect using IPM-compatible tactics for *S. litura* management is a high priority (e.g., biological control, biopesticides, host-plant resistance and non-disruptive conventional insecticides). Tactics should limit the impact on natural enemies, as a build-up of parasitoids and predators during vegetative growth could aid in the control of *H. armigera* and *S. frugiperda* populations when they arise during reproductive crop stages, along with potentially helping to manage other capsicum pests (e.g., whitefly, mites, thrips and fruit flies).

In terms of *H. armigera* management, our data indicate that there may only be a brief window where *H. armigera* populations successfully establish in the crop—flowering. Therefore, sampling and management decisions should be focused on the flowering stage where moths are most attracted to the crop and neonate larvae are most likely to survive. Close monitoring during this stage could enable detection of *H. armigera* eggs and early instar larvae before they become entrenched in fruits.

Finally, we can infer that *S. frugiperda* is unlikely to warrant treatment during vegetative growth stages. The risk of *S. frugiperda* entering fruit appears greatest during the early and mid-fruiting stages, where larvae will preferentially move to the fruit. Infestations in capsicum fruits likely arise from early instar larvae, as first instars can penetrate the fruit wall to feed inside the fruit. Monitoring for *S. frugiperda* during fruiting is essential, and searches should be focused on looking for larvae/feeding damage underneath the fruit calyx or at the apex of the fruit. Potential management strategies to decrease pest oviposition and maximise egg/neonate mortality could include trap cropping, mating disruption and biological control. However, given that *S. frugiperda* moths do not prefer to oviposit on capsicum plants, further research is required to elucidate the scenarios under which capsicum crops are infested with this species. For instance, are nearby source crops or weeds generating *S. frugiperda* populations that then spill over into capsicum crops as larvae disperse from these source crops?

In conclusion, the data we obtained in this study through a series of simple glasshouse experiments documented clear differences in how three noctuid pest species infest capsicum plants. These results have elucidated how larval infestations in capsicum fruits arise and should help refine management strategies which have previously been dependent on prophylactic insecticide applications. From our results there are obvious research opportunities to guide the further development of strategies to more effectively manage these pests in the field (e.g., developing rigorous sampling techniques during flowering/fruiting stages and investigating non-chemical management strategies during vegetative crop stages). This study has also highlighted how little fundamental information there is available to understand the interactions between major crop plants and their key lepidopteran pest species, as well as the relative ease with which such information can be generated.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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