EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **123**: 148–157, 2026
doi: 10.14411/eje.2026.015
ORIGINAL ARTICLE

Inter- and intraspecific variation in cannibalism in seed bugs (Hemiptera: Lygaeidae)

MADINGLEY M. ABBS, ANGELOS PECHLIVANIS, LEILA M. COOPER, ELEANOR H.Z. GOUREVITCH and DAVID M. SHUKER

Centre for Biological Diversity, Sir Harold Mitchell Building and Dyers Brae, University of St Andrews, St Andrews, Fife, KY16 9TH, UK; e-mails: mm.abbs@outlook.com, apechlivanis@merresearch.com, leilamariecooper@hotmail.co.uk, ehzgourevitch@gmail.com, david.shuker@st-andrews.ac.uk

Key words. Ecology, starvation, learning, developmental stage, *Spilostethus pandurus*

Abstract. Whilst common across the animal kingdom, the evolution of cannibalism remains poorly understood. Part of the problem is that the number of taxonomic groups in which the evolution of cannibalism has been studied in detail is limited, leaving us with only patchy data to explore trends across species. In this study, we consider within and between species variation in cannibalism in four species of seed bug with similar but not identical ecologies. Looking first at the influence of developmental stage on cannibalism, we show that cannibalism is generally most common in juvenile stages of these species, being especially pronounced in some cases early in life (when further dispersal is likely typically needed to locate host plants). Closer examination of one of these species, *Spilostethus pandurus*, suggests that cannibalism has evolved specifically as an adaptation to early life survival and not a general trait for starvation resistance across the lifetime. Cannibalism propensity was also observed to depend on early life experience of conspecifics in this species, suggesting a role for environmental variation in shaping this behaviour. These results highlight that if we are to understand trends in cannibalism across the animal kingdom, we must consider the ecological causes of variation in cannibalism within and between species.

INTRODUCTION

Cannibalism is a commonly observed behaviour across a wider diversity of taxa (including birds: Ingram (1959), arachnids: Bilde & Lubin (2001), amphibians: Garza & Waldman (2015), and insects: Collie et al., 2013). Cannibalism may influence population dynamics (Claessen et al., 2004) and can have both economic (Liu et al., 2017) and environmental impacts (Javidpour et al., 2020). Moreover, cannibalism has strong links with evolutionary theory such as Hamilton's Rule (Perry & Roitberg, 2005), and research on this area is also linked to other aspects of behavioural ecology such as sexual selection and mating systems (through sexual cannibalism: Wilder et al., 2009; Dougherty et al., 2013), parental care (through filial cannibalism and matriphagy: Kim et al., 2000; Deal & Wong, 2016) and sibling rivalry (through sibling cannibalism: Mock & Parker, 1997; Pfennig, 1997).

Here we take a broad definition of cannibalism, considering it to be the consumption (either wholly or in part) of conspecifics. This is inclusive of cannibalism in the strictest sense, where conspecific individuals are killed by the cannibal prior to being eaten (following Elgar & Crespi, 1992) but also includes other cannibalistic behaviours such as the consumption or scavenging of already dead conspecifics [as is observed in some cases of human cannibalism (Mathews, 2008) and cannibalism in non-human animals (Allen et al., 2022)] and the partial consumption of live individuals (the partial sexual cannibalism of male hindwings by female sagebrush crickets during copulation being a famous example of this: Johnson et al., 1999).There are two main hypotheses for the evolution of cannibalism, namely nutritional benefits and competition reduction (Richardson et al., 2010). Additionally, factors such as disease risk and the (inclusive fitness) costs of consuming a relative in the case of sibling cannibalism can select against cannibalism (Pfennig, 1997), although these relationships are not necessarily straightforward [for further discussion see Van Allen et al. (2017) and Garay et al. (2016)]. Most importantly, it is not currently clear why cannibalism is common across taxonomic groups, but rather rare within them (Elgar & Crespi, 1992). Furthermore, whilst much is known about the propensity or not of different species to avoid cannibalising relatives (for example see Baur, 1987a; Anderson & Solbreck, 1992; Bilde & Lubin, 2001; Michaud, 2003; Fea et al., 2014; Abbs et al., 2025), we do not have a good enough understanding of sibling cannibalism to explain the trends observed across taxa in terms of the presence and absence of kin discrimination during cannibalism. In particular, we need detailed within- and among-species studies of variation in cannibalism. While some systems have indeed been well-studied, such as sexual cannibalism in spiders (e.g. Bilde et al., 2006) and mantids (Brown & Barry, 2016), and sibling cannibalism in ladybirds (Omkar et al., 2007), in general the cannibalism literature is still largely anecdotal in nature (Elgar & Crespi, 1992; Soulsby, 2013).

Here we consider inter- and intraspecific variation in cannibalism across four species of lygaeid seed bug (Hemiptera: Lygaeidae). Seed bugs are a globally distributed family of mostly plant-feeding hemipterans in which some instances of cannibalistic behaviour have been recorded and studied (Root & Chaplin, 1976; Root, 1986; Solbreck & Sillén-Tullberg, 1990; Anderson & Solbreck, 1992; Burdfield-Steel & Shuker, 2014). We studied four species: *Lygaeus simulans* (Deckert, 1985), *L. equestris* (Linnaeus, 1758), *L. creticus* (Lucas, 1854) and *Spilostethus pandurus* (Scopoli, 1763). Two of these species, *S. pandurus* and *L. creticus*, have been studied in terms of the role of kin discrimination in sibling cannibalism. In both cases, there was an absence of kin discrimination during egg cannibalism, which was attributed to the substantial survival benefits of consuming an egg (and hence satisfying Hamilton's Rule for the evolutionary benefit of eating a sibling: Anderson & Solbreck, 1992; Abbs et al., 2025).

First, we recorded variation in cannibalism propensity within and between these four species, to explore how species and individual developmental stages vary in terms of their cannibalism propensity. Previous quantitative studies of cannibalism in lygaeids have been restricted to newly hatched individuals (Anderson & Solbreck, 1992; Abbs et al., 2025), with little consideration of how this behaviour may vary across development. Following patterns observed in other insect species (Omkar et al., 2007; Schausberger & Hoffmann, 2008; Collie et al., 2013), we expected cannibalism to be highest early in juvenile development (i.e. first or second nymphal instar). Second, focusing on one of the species found at our Sicilian field sites, *S. pandurus*, we examined ways in which an individual's environment influenced its likelihood of cannibalism. Following results in *S. pandurus* and *L. creticus* that cannibalism reduces mortality rate for first instar nymphs (Anderson & Solbreck, 1992; Abbs et al., 2025), we assessed the influence of the interaction between starvation and developmental stage, expecting starvation to drive higher cannibalism levels. Finally, we also assessed the role of early life experience of conspecific eggs on cannibalism propensity, to test whether previous opportunity for cannibalising, or experience of an egg, influenced later cannibalistic behaviour.

METHODS

Lygaeid husbandry

We focused on four species of seed bug: *Lygaeus simulans*, *L. equestris*, *L. creticus* and *Spilostethus pandurus*. All four species display five juvenile developmental stages (termed nymphs) and the adult stage. Importantly, all four species also display black-and-red aposematic coloration across all life stages, signalling to potential predators their toxic chemical defences (Burdfield-Steel et al., 2013; Burdfield-Steel & Shuker, 2014). These insects sequester these toxins from the seeds and other tissues of their foodplants (Burdfield-Steel et al., 2013; Burdfield-Steel & Shuker, 2014), which form a key part of their nutritional ecology. In their natural environment these species typically feed on members of the Apocynaceae, although they may also consume other cardenolide-containing plants from other families and can be found on a range of other plants including some crop plants (Sweet II, 2000; Burdfield-Steel et al., 2013; Burdfield-Steel & Shuker, 2014; Havlikova et al., 2020; Pokharel et al., 2021; Cianferoni & Dia, 2023). Whilst ostensibly herbivorous, plant-feeding lygaeids may also be opportunistic scavengers and predators, thanks to their piercing and sucking mouthparts, including in terms of intra-guild predation and cannibalism (Burdfield-Steel & Shuker, 2014).

Laboratory populations were obtained from wild populations of bugs (*Lygaeus simulans*: Tuscany, Italy, 2008–2009; Balfour et al., 2020, *L. equestris*: the Dolomites, Italy, 2004; Burdfield-Steel et al., 2013, *L. creticus* and *Spilostethus pandurus*: Sicily, Italy, 2004–2008; Shuker et al., 2015) and maintained in plastic boxes (30 × 15 × 15 cm) with sunflower seeds ad libitum, a square of cotton wool and distilled water contained within two-three 25 ml plastic tubes stoppered with cotton wool. We replaced water tubes once a week, replacing population boxes once every two to three months. For this process, we transferred bugs of all stages to a fresh population box using a pooter, taking care to include bugs from multiple existing population boxes in this new population to prevent inbreeding. Population boxes were stored in incubators at 29°C on a 22L : 2D cycle which prevents reproductive diapause from occurring (Balfour et al., 2020).

Experiment 1: Developmental variation in cannibalism in four species of seed bug

In this experiment we compared the levels of egg cannibalism across all five nymphal instars plus adult males and females for all four species. We considered cannibalism to be any consumption of egg material, either observed directly through behavioural observations of egg feeding (for further explanation see below) or indirectly through observations of eggs following cannibalism trials (again, described in greater detail below). Whilst data (such as fertilisation status, see below) on eggs was recorded during trials, we did not distinguish by egg type when recording cannibalism, and as such cannibalism is considered to be the consumption of clearly fertilised eggs and eggs which are either unfertilised or in the early stages of development.

Egg collection

To generate the target eggs for consumption, we placed adult bugs of each species in small tubs (108 × 82 × 55 mm) with sunflower seeds and 7 ml universal tubes of distilled water stoppered with cotton wool. Approximately ten bugs (five male and five female) were left in each tub to mate, with tubs being stored in incubators at 29°C and checked for eggs every two days. When eggs were present, we transferred all bugs to a new and identical tub, with the tubs containing eggs being stored in incubators for future use in experiments. Dead bugs were replaced with individuals of the corresponding sex and species.

Pre-treatment

Bugs of each species and developmental stage were randomly selected from stock populations and left individually in empty plastic tubs overnight (approximately 17 h). This was done to provide a degree of standardisation to the nutritional and hydration experience of focal "cannibals" prior to experimental cannibalism trials. Adults were likewise selected randomly.

Cannibalism trials

We placed focal individuals alone in 55 mm Petri dishes with five conspecific eggs. We recorded the number of days since egg collection and also egg fertilisation status (fertilisation is indicated by a colour change of cream to orange-red, with cream eggs either being unfertilised or too early in development for fertilisation status to be detected). No eggs were used which had been collected over 7 days previously, and care was taken to ensure eggs were not damaged before use. Cannibalism trials lasted four hours. To give us a better idea of the types of behaviours displayed, we recorded cannibalism and its associated behaviours (such as mounting and feeling an egg with the rostrum) continuously for the first hour of the four-hour trials. Additionally, for the next three hours we used a scan-sampling approach, recording whether bugs were cannibalising (rostrum inserted into egg for 15 s or longer) or mounting eggs (was standing over or making contact with an egg, includes cases where rostrum is inserted into egg and where no rostrum insertion has occurred) at 15-minute intervals until the full four-hour trial was completed. At the end of the four-hour trial, bugs were removed and euthanised, and the number of eggs each individual had cannibalised was recorded (with cannibalism scored as material having been visibly removed from eggs, which was checked under a dissecting microscope). We obtained several measures of cannibalism and its associated behaviours from these experiments. The proportion of individuals displaying cannibalism included cases where cannibalism was observed both behaviourally and in observations of eggs (described above) at the end of trials. The proportion of individuals displaying mounting and the proportion of time spent mounting/cannibalising were measures derived from the behavioural observations only whereas the proportion of eggs consumed was a measure derived entirely from the end of trial egg observations. Across the experiment, N = 434 bugs were tested, with sample sizes per species and instar ranging from N = 13–18 in juveniles and N = 28–31 in adults (full sample size details are given in Table S1).

Experiment 2: The influence of food availability and developmental stage on cannibalism in *S. pandurus*

In this experiment, we tested how food availability and developmental stage influenced the level of egg cannibalism in *S. pandurus*. Results from Experiment 1 indicated that *S. pandurus* appeared to be one of the more cannibalistic of our four species at the first instar stage, identifying it as a good candidate for future experimental work on cannibalism. Cannibalism was defined as with Experiment 1, including with regards to the type of egg consumed.

Egg collection

Target *S. pandurus* eggs were collected by storing adults in tubs as in Experiment 1, checking for eggs everyday Monday–Friday. When present, eggs were removed and placed in egg collection boxes for later use in experimental trials.

Treatments

There were two experimental treatments: Developmental stage and Starvation. In terms of developmental stage, we used first, third, and fifth instar nymphs, plus adults. In terms of starvation, individuals were either “Starved” or “Not-starved”. Individuals of the appropriate developmental stage were randomly selected from stock populations as before. However, not-starved individuals were taken from stock populations and placed directly into cannibalism trials with no prior treatment. We placed starved individuals in tubs for two days with distilled water (held in cotton wool stoppered 7 ml universal tubes) but no food prior to use in cannibalism trials. The experiment was fully factorial.

Cannibalism trials

We used the same experimental protocol for the cannibalism trials as in Experiment 1, with the following alterations: we used ten eggs instead of five, scoring cannibalism as before. For the larger scale Experiment 1 we used fewer eggs per replicate, but the data from both Experiments 1 and 2 showed that five eggs was more than sufficient to capture variation in egg cannibalism over four hours, hence we reverted to using five eggs for Experiment 3 (see below). Focal individuals were placed alone into Petri dishes as with Experiment 1. The sample sizes were: Adults (Starved, N = 27 and Not Starved, N = 27) and first (Starved, N = 9 and Not Starved, N = 10), third (Starved, N = 9 and Not Starved, N = 10) and fifth instar (Starved, N = 9 and Not Starved, N = 10).

Experiment 3: The influence of prior experience on cannibalism in *S. pandurus* nymphs

In our third experiment, we considered how access to, and consumption of, eggs by first instar *S. pandurus* nymphs influenced cannibalism at the third instar stage. Cannibalism was defined as with Experiments 1 and 2.

Egg collection

We collected eggs using the same methods as Experiments 1 and 2.

Treatments

To obtain experimental nymphs, we separated eggs upon fertilisation into individual plastic tubs with 25–35 sunflower seeds and a 7 ml universal tube of distilled water, recording the natal clutch of each egg. Upon hatching, first instar nymphs were placed in one of two treatments. In the early exposure treatment (E), we placed nymphs in 55 mm ventilated Petri dishes with five conspecific eggs for four hours, as per Experiment 1. Cannibalism was scored as in Experiments 1 and 2. The overall sample size for the E treatment was N = 95, later subdivided into those individuals who cannibalised, N = 64, and those who did not, N = 31 (see below). In the no early exposure treatment (U), N = 49 first instar nymphs were placed in empty 55 mm ventilated Petri dishes for four hours with no conspecific egg exposure. Nymphs from both treatments were then allowed to develop to the third instar stage (in plastic tubs with 25–35 sunflower seeds and a 7 ml tube of distilled water, stored at 29°C) before being placed into cannibalism trials as per the methods of Experiment 1. Focal individuals were placed alone into Petri dishes as with Experiment 1.

Statistical analysis

All analyses were completed in R version 4.5.1 (R Core Team, 2025). All Generalised Linear Mixed Models (GLMM’s) were provided by the *lme4* and *blme* packages, and we used the *car* package to test the significance of the fixed effects using Type II sums of squares.

Experiment 1

We tested for the effect of developmental stage, species, and their interaction on the proportion of individuals which displayed cannibalism and the proportion of individuals which displayed mounting (binomial Generalised Linear Model (GLM) with a logit link function). For the subset of individuals which displayed cannibalism, we also tested for the effect of developmental stage, species, and their interaction on the proportion of eggs consumed from a clutch and the proportion of time spent cannibalising (again using binomial GLM’s). This analysis was also completed for the proportion of time spent mounting by those individuals who displayed mounting. Both linear, quadratic and cubic terms were tested for developmental stage, in case there were any non-linear relationships between development and cannibalism. We used Akaike Information Criterion (AIC – provided by the *MuMIn* package) to assess model fit, and quadratic or cubic terms dropped from models as necessary. To keep our Results section as streamlined as possible, when either quadratic or cubic terms are not mentioned, only linear terms were fitted. In all cases we assessed if experimenter needed to be controlled for as a random effect (using Generalised Linear Mixed Models, GLMM'S, instead of GLM's), however we found there to be very little variation in our results that were attributable to experimenter, and therefore this term was dropped from all analyses for this experiment. We additionally tested for any confounding effects of egg fertilisation status (fertilised or unfertilised/in the early stages of development) on our results. However, after finding negligible effects (P values ranging from P = 0.95 to P = 0.16), this too was dropped from all analyses. Adults were also originally considered separately by sex in our analysis. However, adult cannibalism levels were too low for any meaningful comparisons between the sexes (Proportion of individuals displaying cannibalism ranged from 0–0.13 for both males and females, see below), and therefore male and female adults were combined into one single adult group.

Experiment 2

We assessed the effect of developmental stage, starvation treatment, and their interaction on the probability individuals displayed mounting, the probability individuals displayed cannibalism, the proportion of eggs consumed by those individuals' displaying cannibalism, the proportion of time those individuals who cannibalised spent cannibalising, and the proportion of time those individuals who mounted eggs spent mounting (binomial Generalised Linear Model (GLM) with logit link function). As with Experiment 1, we tested for both linear, quadratic and cubic terms for developmental stage, using AIC (provided by the *MuMIn* package) to select the best fitting model. Results of model selection are reported as with Experiment 1. Cubic terms could not be tested for the proportion of eggs consumed and the proportion of time spent cannibalising as the underlying data sets were likely too limited for the level of model complexity as the models struggled to fit. As such only linear and quadratic terms were tested for these measures of cannibalism and associated behaviour.

Experiment 3

We assessed the effect of egg experience ("E" treatment vs "U" treatment) and cannibalism experience (Cannibalism displayed, "C", No cannibalism displayed, "NC", and No prior egg experience, "U") at the first instar stage on the probability of mounting and cannibalising at the third instar stage using binomial GLM's with a logit link function. As before, the effect of prior egg experience and prior cannibalism experience on the proportion of eggs consumed by those individuals which displayed cannibalism, the proportion of cannibalism trials spent cannibalising by those individuals which displayed cannibalism, and the proportion of cannibalism trials spent mounting by those individuals which displayed egg mounting, was tested using binomials GLM's. Similarly to Experiment 1, the egg clutch a focal nymph originated from was included as a random effect in initial statistical tests for all measures, using GLMM'S. Clutch was however found to cause very little variation in the data and as such the random effect was not included in the final models. As with Experiment 1, effects of egg fertilisation status were also tested for and again found to be negligible (P values ranging from P = 0.20 to P = 0.99).

RESULTS

Experiment 1

Across the four species, patterns of cannibalism were influenced by both developmental stage and species. The proportion of individuals displaying cannibalism showed no variation with developmental stage in isolation (linear term: $\chi^2_1 = 1.14$, P = 0.29, quadratic term: $\chi^2_1 = 0.08$, P = 0.77) but the effect of developmental stage on the proportion of individuals displaying cannibalism did vary by species, with significant interactions with developmental stage in terms of both linear and quadratic terms in the model (Species × Developmental stage: linear term for developmental stage: $\chi^2_3 = 13.06$, P = 0.005, quadratic term for developmental stage: $\chi^2_3 = 14.11$, P = 0.003; Fig. 1a). Cannibalism propensity was similar for instar stages one to four in *L. creticus*, although cannibalism was absent from fifth instars and adults. For *L. equestris* cannibalism propensity peaked at the third instar stage. In both *L. simulans* and *S. pandurus* cannibalism was highest at the first instar stage, although this effect was much more pronounced for *S. pandurus* (Fig. 1a).

For those individuals who displayed cannibalism, the proportion of eggs consumed showed a general trend of increasing and then declining as development progressed, although this effect of developmental stage was not significant (linear term $\chi^2_1 = 1.87$, P = 0.17) nor was the interaction between developmental stage and species (linear term $\chi^2_3 = 4.61$, P = 0.20; Fig. 1b). The proportion of time spent cannibalising was affected by developmental stage (linear term: $\chi^2_1 = 16.79$, $P < 0.001$), with the exact influence of development on this measure being further shaped by species (Species × Developmental stage interaction: linear term: $\chi^2_3 = 14.99$, P = 0.002). Whilst patterns across the juvenile period were variable, all four species generally showed a decline in the proportion of time spent cannibalising leading up to adulthood (Fig. 1c).

Cannibalism behaviour mostly did not differ among the four species independently of effects associated with developmental stage: the proportion of individuals displaying cannibalism (Species: $\chi^2_3 = 3.32$, P = 0.34), the proportion of egg consumed by cannibalistic individuals (Species: $\chi^2_3 = 6.75$, P = 0.08) or the proportion of time spent cannibalising (Species: $\chi^2_3 = 7.02$, P = 0.07; Fig. 1a–c).

Egg mounting propensity showed significant variation across developmental stage (linear term: $\chi^2_1 = 6.53$, P = 0.011, quadratic term: $\chi^2_1 = 6.5$, P = 0.011), however there was no significant influence of species ($\chi^2_3 = 7.72$, P = 0.05), nor a significant interaction between developmental stage and species (interaction with the linear term: $\chi^2_3 = 5.46$, P = 0.14; with the quadratic term: $\chi^2_3 = 4.43$, P = 0.22). *L. creticus* and *S. pandurus* showed the clearest patterns of decreasing followed by increasing mounting propensity across development, with *L. simulans* and *L. equestris* showing no clear trends in mounting propensity as development proceeded (Fig. 2a). For those individuals who did display mounting, generally the proportion of time was lower for the more developed stages, but again there was quite a lot of variation. Statistically, the effect of developmental stage on the proportion of time spent mounting significantly varied across species (Species × Developmental stage: linear term: $\chi^2_3 = 23.40$, $P < 0.001$; quadratic term: $\chi^2_3 = 23.65$, $P < 0.001$; cubic term: $\chi^2_3 = 23.67$, $P < 0.001$). There was however no effect of species ($\chi^2_3 = 6.86$, P = 0.076) or developmental stage (linear term: $\chi^2_1 = 1.83$,

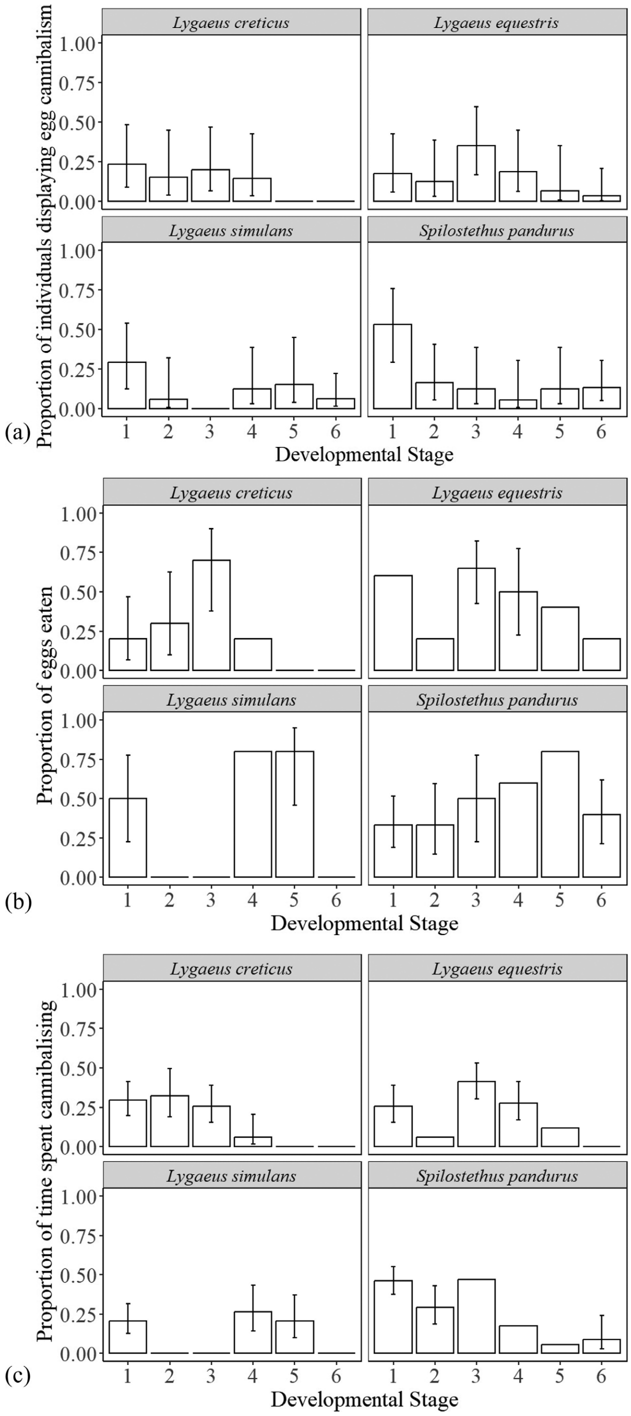

Fig. 1. Species and developmental stage variation in egg cannibalism (errors bars represent ± 95% confidence intervals calculated on the logit scale) in four species of lygaeid seed bug, *Lygaeus creticus*, *L. simulans*, *L. equestris* and *Spilostethus pandurus*. Developmental stages correspond to instars one-five and adults (six). (a) The proportion of individuals displaying egg cannibalism, (b) the proportion of eggs eaten, and (c) the proportion of time spent cannibalising from those individuals who cannibalised.

P = 0.18; quadratic term: $\chi^2_1 = 1.29$, P = 0.26; cubic term: $\chi^2_1 = 1.62$, P = 0.20) in isolation on this measure (Fig. 2b).

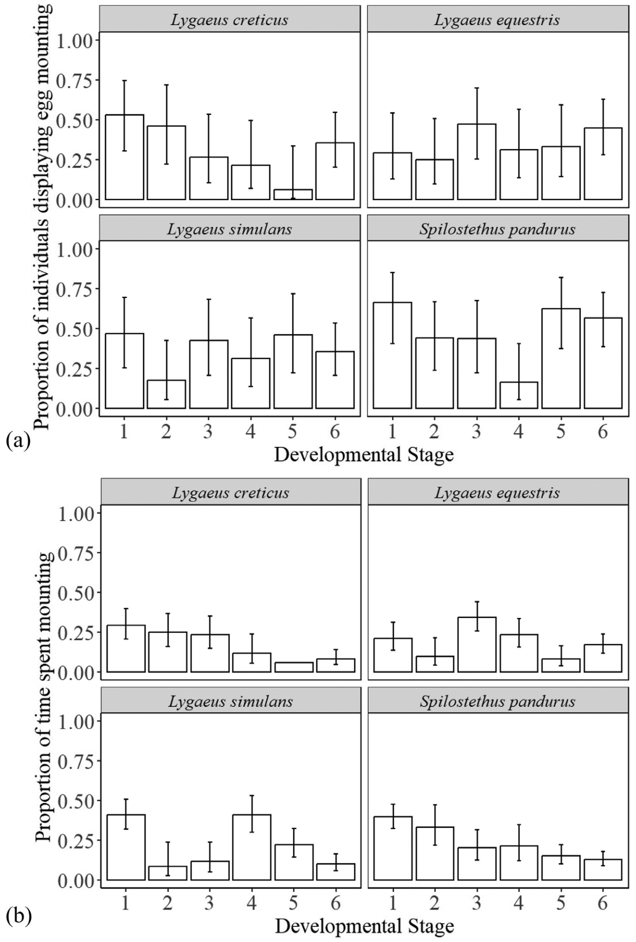

Fig. 2. Variation in egg mounting across different species and developmental stages (instars one-five and adults, six) of four lygaeid seed bugs: *Lygaeus creticus*, *L. simulans*, *L. equestris* and *Spilostethus pandurus*. (a) The proportion of individuals displaying egg mounting and (b) the proportion of time spent mounting from those individuals who mounted eggs. ± 95% confidence intervals calculated on the logit scale.

Experiment 2

Developmental stage proved to be a more important correlate of cannibalism than short-term food deprivation in *S. pandurus*. The proportion of individuals displaying cannibalism was significantly affected by developmental stage ($\chi^2_1 = 27.65$, P < 0.001), with a general decrease in cannibalism with developmental stage as seen in Experiment 1. Starvation did not have any significant influence on cannibalism however ($\chi^2_1 = 0.23$, P = 0.63). The effect of developmental stage on cannibalism was also independent of starvation, although we note that this interaction was close to significance (interaction: $\chi^2_1 = 3.02$, P = 0.082; Fig. 3a). For those individuals which did display cannibalism, the proportion of eggs eaten from the clutch of ten eggs did not differ across developmental stage ($\chi^2_1 = 2.81$, P = 0.09). Starvation however did significantly increase the proportion of eggs eaten ($\chi^2_1 = 11.92$, P < 0.001), although not in a manner which varied by developmental stage (Starvation × Developmental stage interaction: $\chi^2_1 = 0.04$, P = 0.85; Fig. 3b). In general, for those individuals who displayed cannibalism, there was a decline in the amount of time spent cannibalising across development, in terms of both linear and quadratic terms, suggesting a curvilinear relationship (linear term: $\chi^2_1 = 94.53$, P < 0.001, quadratic term: $\chi^2_1 =$

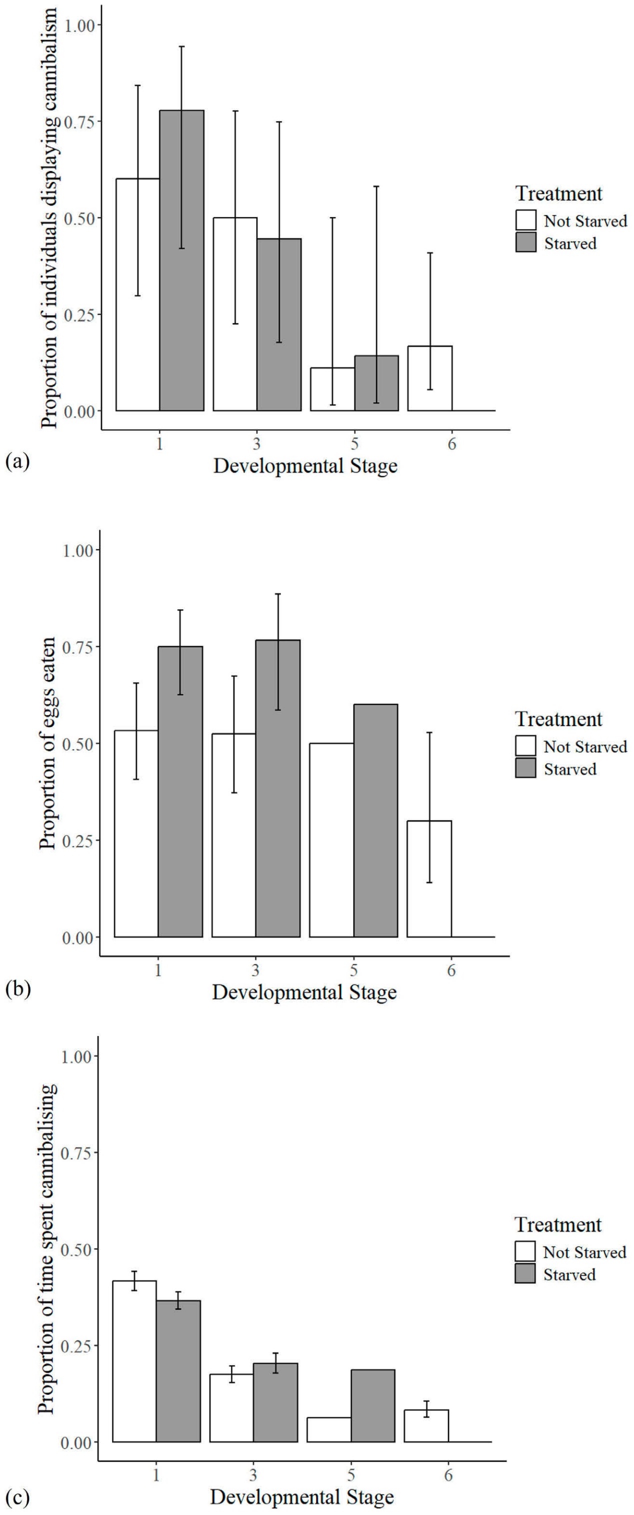

Fig. 3. The effect of starvation and developmental stage on egg cannibalism levels of *Spilostethus pandurus* (± 95% confidence intervals calculated on the logit scale). Three instar stages were tested (one, three, and five) along with the adult stage (six). (a) The proportion of individuals displaying cannibalism (b) from those individuals which cannibalised, the proportion of eggs eaten (c) from those individuals which cannibalised, the proportion of time during cannibalism trials spent cannibalising.

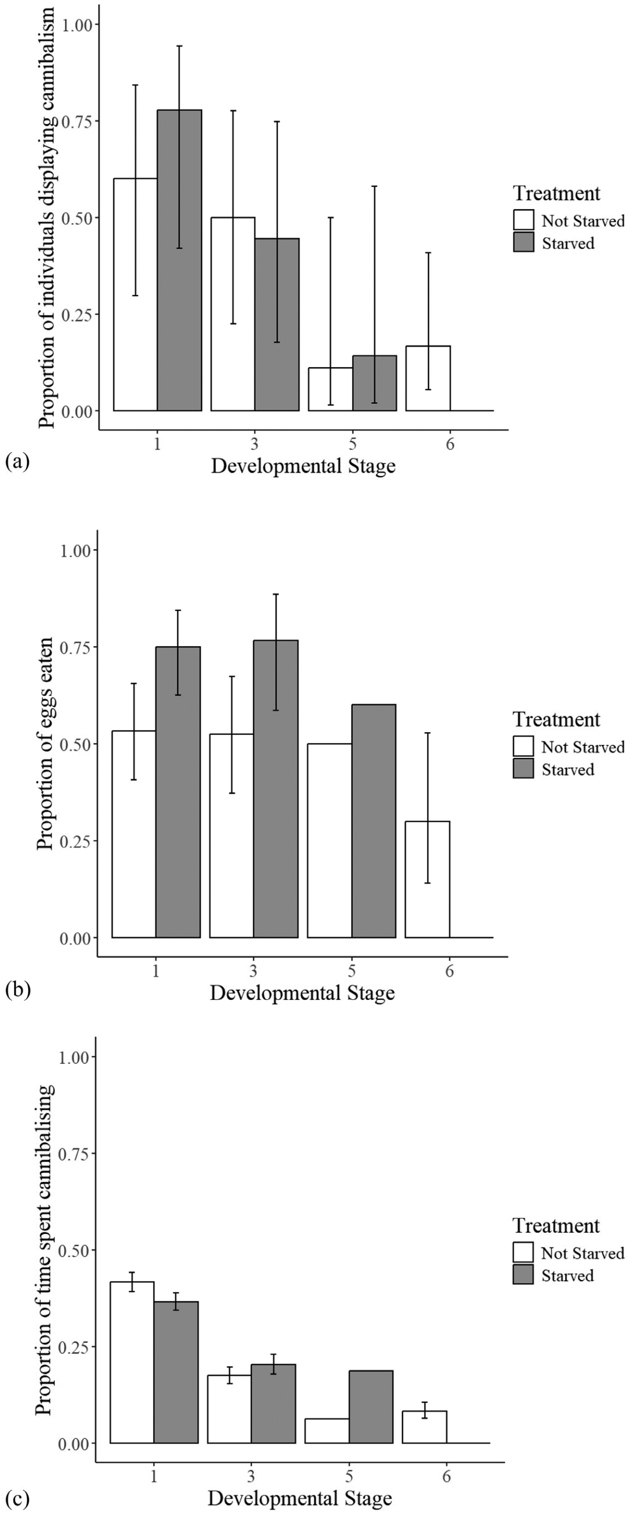

Fig. 4. The effect of starvation and developmental stage on egg mounting in *Spilostethus pandurus* (± 95% confidence intervals calculated on the logit scale). (a) The proportion of individuals mounting (b) from those individuals who mounted, the proportion of time spent mounting. Developmental stages as per Fig. 3.

23.78, $P < 0.001$). Starvation and the interaction between starvation and developmental stage also had no significant effect on the proportion of time spent cannibalising (Starvation: $\chi^2_1 = 0.16$, $P = 0.69$, Starvation × Developmental stage: linear term: $\chi^2_1 = 0.37$, $P = 0.54$, quadratic term: $\chi^2_1 = 0.53$, $P = 0.47$; Fig. 3c).

In terms of egg mounting behaviour, there was no effect of developmental stage, starvation or their interaction on

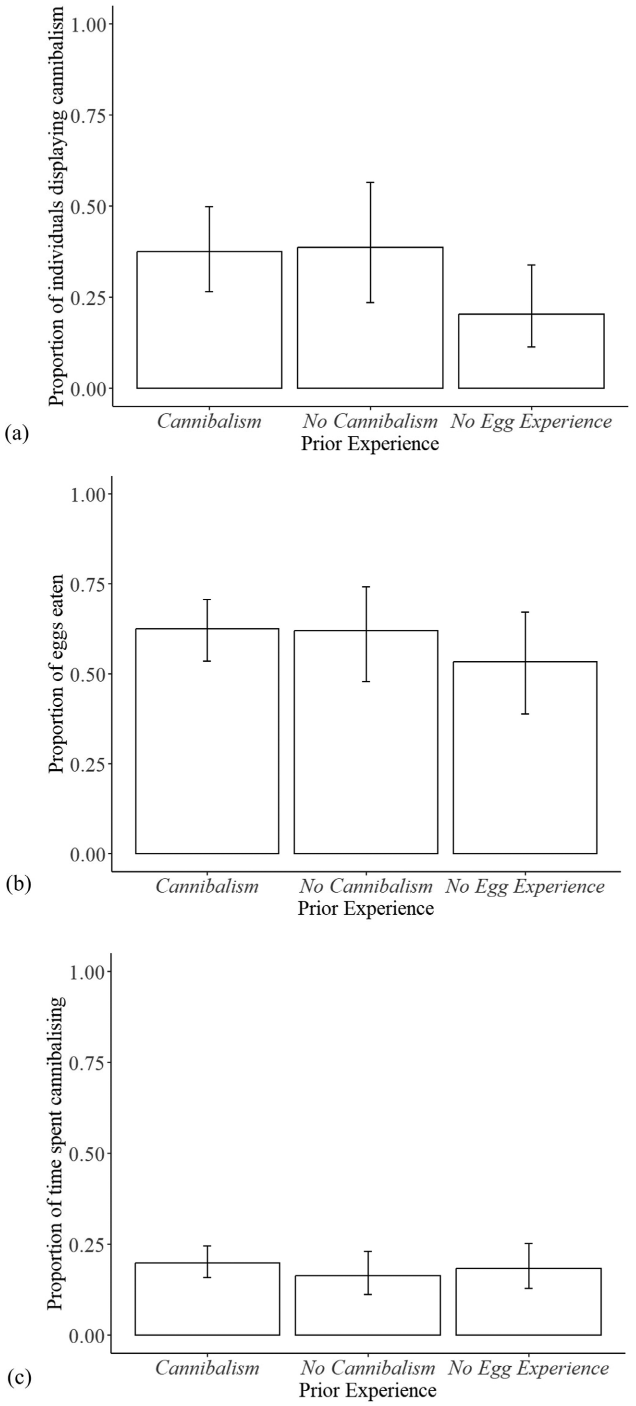

Fig. 5. The effect of prior egg cannibalism experience at the first instar stage on egg cannibalism propensity in third instar *Spilostethus pandurus* nymphs (± 95% confidence intervals calculated on the logit scale). (a) the proportion of individuals displaying cannibalism (b) from those individuals displaying cannibalism, the proportion of eggs consumed (c) from those individuals' displaying cannibalism, the proportion of total cannibalism trial time spent cannibalising.

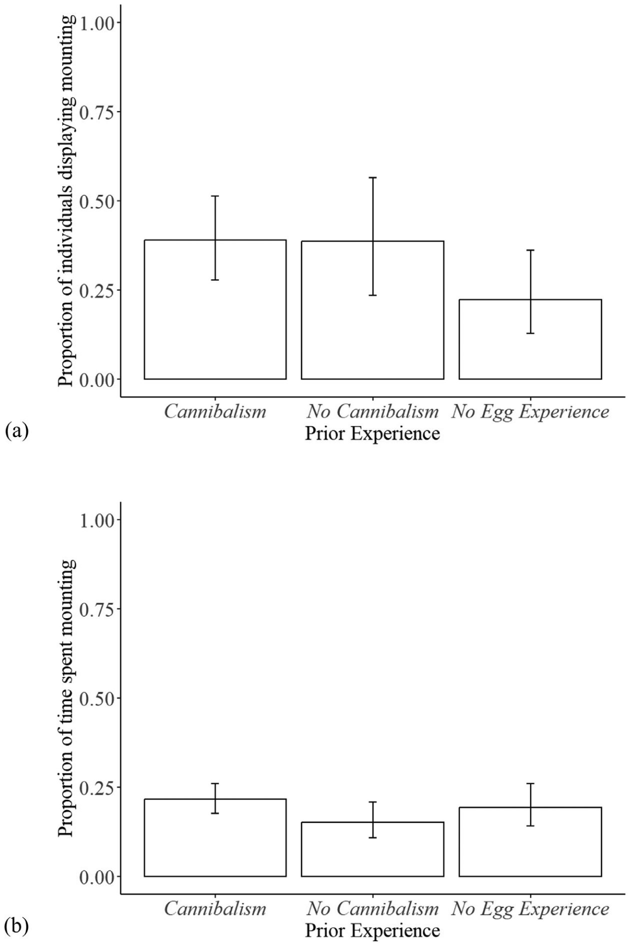

Fig. 6. The effect of prior egg cannibalism experience at the first instar stage on mounting propensity of *Spilostethus pandurus* third instar nymphs (± 95% confidence intervals calculated on the logit scale). (a) The proportion of individuals displaying mounting (b) from those individuals who mounted, the proportion of time spent mounting.

the proportion of individuals that mounted eggs (Developmental stage: $\chi^2_1 = 0.90$, P = 0.34; Starvation: $\chi^2_1 = 0.25$, P = 0.62; Developmental stage * Starvation: $\chi^2_1 = 0.02$, P = 0.88; Fig. 4a). For those individuals that displayed mounting, individuals generally mounted for longer earlier in development, although the exact influence of developmental stage on time spent mounting did depend on starvation (Starvation × Developmental stage interaction: linear term: $\chi^2_1 = 12.87$, P < 0.001, quadratic term: $\chi^2_1 = 14.82$, P < 0.001, cubic term: $\chi^2_1 = 15.49$, P < 0.001). Starvation and developmental stage as main effects were both non-significant with regards to the proportion of time spent mounting (Starvation: $\chi^2_1 = 0.87$, P = 0.35; Developmental Stage: linear term: $\chi^2_1 = 0.49$, P = 0.48, quadratic term: $\chi^2_1 = 1.42$, P = 0.23, cubic term: $\chi^2_1 = 2.96$, P = 0.085; Fig. 4b).

Experiment 3

Previous exposure to conspecific eggs shaped later cannibalism. Third instar *S. pandurus* nymphs were more likely to cannibalise eggs if they had first been exposed to eggs as first instars ($\chi^2_1 = 4.75$, P = 0.029). It did not matter however whether those individuals cannibalised any of the eggs during that initial exposure (i.e. no differences between C and NC individuals: $\chi^2_2 = 4.77$, P = 0.092; Fig. 5a). Exposure to conspecific eggs did not influence the proportion of eggs consumed ($\chi^2_1 = 1.20$, P = 0.27), nor the amount of time spent cannibalising ($\chi^2_1 = 0.012$, P = 0.913), for those individuals who displayed cannibalism. Equally, previous cannibalism also had no effect on either of these measures (proportion of eggs consumed: $\chi^2_2 = 1.2$, $P = 0.55$; proportion of time spent cannibalising: $\chi^2_2 = 0.852$, $P = 0.653$; Fig. 5a, b).

In terms of mounting, exposure again influenced the likelihood of mounting ($\chi^2_1 = 4.11$, $P = 0.043$), but this was likewise independent of whether cannibalism had taken place ($\chi^2_2 = 4.11$, $P = 0.13$; Fig. 6a). For those individuals who displayed mounting, neither egg exposure nor egg cannibalism influenced the proportion of time spent mounting (exposure: $\chi^2_1 = 0.0001$, $P = 0.992$; cannibalism: $\chi^2_2 = 3.63$, $P = 0.16$; Fig. 6b).

DISCUSSION

Much remains to be understood in terms of within and among species variation in cannibalism (see Introduction). Looking across four closely related species of seed bug, we have found significant variation across species in how developmental stage influences cannibalism. While the data are no doubt noisy, the main differences appear to be associated with how much cannibalism is more common in the earliest instars, and the extent to which cannibalism continues across other developmental stages into adulthood (Fig. 1a–c). For instance, whilst *L. creticus* was the most cannibalistic in instar stages one to four, cannibalism in the earliest instars was even more pronounced in *L. simulans* and *S. pandurus*, who displayed the greatest cannibalism propensity as first instars (this trend being the strongest in *S. pandurus*).

All four of our species are closely related (Burdfield-Steel & Shuker, 2014; Shuker et al., 2015) [especially the members of the *Lygaeus* genus, with *L. simulans* and *L. equestris* being sister species (Evans et al., 2015)] with similar ecologies (Burdfield-Steel et al., 2013; Burdfield-Steel & Shuker, 2014; personal observ.). Indeed, wild *S. pandurus* and *L. creticus* occur micro-sympatrically at sites in Sicily and often form mixed species aggregations on and around host plants (Burdfield-Steel & Shuker, 2014; Abbs et al., 2025). Despite this, variation in cannibalism exists across these species, suggesting a role for ecological factors, including perhaps diet specialism, which is known to vary amongst members of this group (Evans et al., 1986; Sweet II, 2000; Burdfield-Steel & Shuker, 2014; Pokharel et al., 2021; Cianferoni & Dia, 2023; Martinović et al., 2023).

That cannibalism may vary across development has been recorded before across a range of animal groups including hemipterans (e.g. *Arma custos*: Wu et al., 2021), arachnids (e.g. *Phytoseiulus persimilis*: Schausberger & Hoffmann, 2008) and gastropods (e.g. *Arianta arbustorum*: Baur, 1987b). Of particular interest are those cases where individuals are most cannibalistic when young, a trend observed here most clearly in *S. pandurus*. Cannibalism can be especially important at this early stage of development, both in acting as an alternative food source when typical food is less accessible (Omkar et al., 2007), and in the improved development and survival it can confer to this life-stage (Schausberger & Hoffmann, 2008; Collie et al., 2013). Whilst we have little knowledge of the early life behaviours of *L. equestris* and *L. simulans*, in the field both *L. creticus* and *S. pandurus* lay their eggs in the leaf litter at the base of *N. oleander* plants. Whilst probably helping eggs and first instar nymphs to avoid predators and parasitoids, this also likely leaves them some distance from their food (Anderson & Solbreck, 1992; Burdfield-Steel & Shuker, 2014), with them needing to find the plant's stems and ascend the plant. Cannibalism may provide an extra nutritional boost to facilitate this crucial early foraging (Abbs et al., 2025), and it is possible we would see similar patterns for our other two species.

Starvation was only a minorly important predictor of cannibalism in *S. pandurus* in Experiment 2, increasing the number of eggs consumed when cannibalism was present, but not affecting the overall likelihood that an individual would be cannibalistic. Although the proposed importance of starvation to promoting cannibalism is frequently supported in the literature (for examples see Mayntz & Toft, 2006 and Petersen et al., 2010), juveniles of the spiders *Tigrosa helluo* and *Agelena labyrinthica* both do not respond to starvation with an increased rate of cannibalism (Roberts et al., 2003; Lesne et al., 2016). This indicates that starvation does not always increase cannibalism propensity across the animal kingdom. In *S. pandurus* developmental stage had a much greater influence (cannibalism propensity decreasing with age, as observed for *S. pandurus* in Experiment 1). Cannibalism in this species is therefore more likely an adaptation for success early in life (as discussed above) than a trait evolved to avoid starvation more generally.

Cannibalism in *S. pandurus* was dependent on early life experience, with those individuals who have had experience of conspecific eggs as first instars being more likely to accept these as food sources at their third instar age (Experiment 3). The effect of individual diet history on egg predation preferences has been tested in multiple species with mixed responses. The ladybirds *Propylea dissecta*, *Coccinella septempunctata* and *Menochilus sexmaculatus* generally showed altered preferences towards conspecific eggs and/or eggs of other ladybird species in response to the egg type they were raised on (Pervez et al., 2021), whilst conversely both the previously tested *Menochilus sexmaculatus* and the snail *Ari. arbustorum* have also been observed showing no evidence for a similar effect of previous cannibalism experience (Baur, 1987b; Yadav et al., 2023). In our study it did not matter whether cannibalism had taken place previously, only if an individual had experienced access to conspecific eggs prior to cannibalism trials. That cannibalism propensity can be influenced by previous experience of conspecifics (without the need for actual consumption of the egg) has been observed in the mite *Ph. persimilis*, juveniles of which are more likely to cannibalise those individuals whom they have not been associated with previously, likely helping to avoid consuming kin (Schausberger, 2005).

The results of Experiment 3 suggest that first instar seed bugs learn to recognise viable food sources based on early life experiences. As there was no effect of previous cannibalism experience on later cannibalism propensity it is unlikely to be associative learning causing this behaviour. If this were the case, we would expect the increased propensity for cannibalism to be reliant on prior consumption of conspecific eggs as the eggs themselves become associated with being a viable food item (Schausberger & Peneder, 2017). It is much more likely to be a non-associative type of learning, such as sensitization, habituation, an induction of preference or imprinting (Boiça Júnior et al., 2017; Schausberger & Peneder, 2017), that underlies the behaviour seen here. In this generalist species (Burdfield-Steel & Shuker, 2014), it is possible that the effect seen here is not a case of learning evolved specifically in the context of cannibalism, but more likely a generalised adaptation for nymphs to identify suitable food sources early in life (learning may be particularly useful for more generalist species: Jones & Agrawal, 2017). Regardless of the mechanism or underlying cause, this result shows how the environment, and not just factors intrinsic to a given species, can influence their cannibalistic behaviours.

In our current study we have observed variation in cannibalism propensity within and between several species of lygaeid seed bug with relatively similar ecologies. This variation can be caused by factors intrinsic to a species, such as developmental stage, and by the surrounding environment an individual experiences early in life. Cannibalistic behaviours will likely vary between populations. This study highlights that when evaluating the cannibalism propensities of wild animals, the specific ecological context a surveyed population is experiencing must be considered if we are to properly understand patterns of within and between species diversity in cannibalism.

ACKNOWLEDGEMENTS. We would like to thank T. Green for experimental assistance. This work was supported by a Natural Environment Research Council IAPETUS2 PhD studentship held by M.M. Abbs (grant reference NE/S007431/1). We are also very grateful for the comments of the anonymous reviewers and editor who helped improve our manuscript.

DATA AVAILABILITY. Research data and underlying analysis code is available on PURE (The University of St Andrews' research information system) at https://doi.org/10.17630/6c388b43-4b4d-443b-8ec5-52713103c9f3.

AUTHOR CONTRIBUTIONS. MMA – Experiment 1 design and data collection, Experiment 2 supervision and data collection, Experiment 3 supervision, data analysis, manuscript preparation. AP – Experiment 1 data collection, Experiment 3 design and data collection. LMC – Experiment 2 design and data collection. EHZG – Experiment 2 supervision and data collection. DMS – Experiment 1, 2 and 3 supervision, data analysis, manuscript preparation.

DECLARATION OF INTEREST. The authors have no conflicts of interest to declare.

REFERENCES

Abbs M.M., Kennedy J.R., Drago A. & Shuker D.M. 2025: Hamilton's Rule predicts sibling cannibalism in a wild population of insects. — *Anim. Behav.* **224**: 123196, 7 pp.

Allen M.L., Krofel M., Yamazaki K., Alexander E.P. & Koike S. 2022: Cannibalism in bears. — *Ursus* **33**: e10, 10 pp.

Anderson D.B. & Solbreck C. 1992: Who eats whom? Complex interactions between an egg parasitoid and its cannibalistic host. — *Oikos* **63**: 459–464.

Balfour V.L., Black D. & Shuker D.M. 2020: Mating failure shapes the patterns of sperm precedence in an insect. — *Behav. Ecol. Sociobiol.* **74**: 25, 14 pp.

Baur B. 1987a: Can cannibalistic hatchlings of the land snail *Arianta arbustorum* distinguish between sib and non-sib eggs? — *Behaviour* **103**: 259–265.

Baur B. 1987b: Effects of early feeding experience and age on the cannibalistic propensity of the land snail *Arianta arbustorum*. — *Can. J. Zool.* **65**: 3068–3070.

Bilde T. & Lubin Y. 2001: Kin recognition and cannibalism in a subsocial spider. — *J. Evol. Biol.* **14**: 959–966.

Bilde T., Tuni C., Elsayed R., Pekár S. & Toft S. 2006: Death feigning in the face of sexual cannibalism. — *Biol. Lett.* **2**: 23–25.

Boiça Júnior A.L., Souza B.H.S., Costa E.N. & Paiva L.B. 2017: Influence of fall armyworm previous experience with soybean genotypes on larval feeding behavior. —*Arthropod-Plant Interact.* **11**: 89–97.

Brown W.D. & Barry K.L. 2016: Sexual cannibalism increases male material investment in offspring: Quantifying terminal reproductive effort in a praying mantis. — *Proc. Biol. Sci.* **283**: 20160656, 6 pp.

Burdfield-Steel E.R. & Shuker D.M. 2014: The evolutionary ecology of the Lygaeidae. — *Ecol. Evol.* **4**: 2278–2301.

Burdfield-Steel E.R., Dougherty L.R., Smith L.A., Collins L.A. & Shuker D.M. 2013: Variation in social and sexual behaviour in four species of aposematic seed bugs (Hemiptera: Lygaeidae): The role of toxic and non-toxic food. — *Behav. Process.* **99**: 52–61.

Cianferoni F. & Dia A. 2023: First records of *Lygaeus creticus* Lucas, 1854 for Lebanon and several Mediterranean islands, with remarks on some distribution records. — *Heteroptera Poloniae – Acta Faunistica* **17**: 55–59.

Claessen D., de Roos A.M. & Persson L. 2004: Population dynamic theory of size-dependent cannibalism. — *Proc. Biol. Sci.* **271**: 333–340.

Collie K., Kim S.J. & Baker M.B. 2013: Fitness consequences of sibling egg cannibalism by neonates of the Colorado potato beetle, *Leptinotarsa decemlineata*. — *Anim. Behav.* **85**: 329–338.

Deal N.D.S. & Wong B.B.M. 2016: How mate availability influences filial cannibalism. — *Q. Rev. Biol.* **91**: 47–67.

Dougherty L.R., Burdfield-Steel E.R. & Shuker D.M. 2013: Sexual stereotypes: The case of sexual cannibalism. — *Anim. Behav.* **85**: 313–322.

Elgar M.A. & Crespi B.J. (eds) 1992: *Cannibalism: Ecology and Evolution Among Diverse Taxa*. Oxford University Press, Oxford, 361 pp.

Evans D.L., Castoriades N. & Badruddine H. 1986: Cardenolides in the defense of *Caenocoris nerii* (Hemiptera). — *Oikos* **46**: 325–329.

Evans G.M.V., Nowlan T. & Shuker D.M. 2015: Patterns of reproductive isolation within and between two *Lygaeus* species characterized by sexual conflicts over mating. — *Biol. J. Linn. Soc.* **116**: 890–901

Fea M.P., Stanley M.C. & Holwell G.I. 2014: Cannibalistic siblicide in praying mantis nymphs (*Miomantis caffra*). — *J. Ethol.* **32**: 43–51.

Garay J., Varga Z., Gámez M. & Cabello T. 2016: Sib cannibalism can be adaptive for kin. — *Ecol. Model.* **334**: 51–59.

Garza S. & Waldman B. 2015: Kin discrimination in polyphenic salamander larvae: Trade-offs between inclusive fitness and pathogen transmission. — *Behav. Ecol. Sociobiol.* **69**: 1473–1481.

Havlikova M., Bosakova T., Petschenka G., Cabala R., Exnerova A. & Bosakova Z. 2020: Analysis of defensive secretion of a milkweed bug *Lygaeus equestris* by 1D GC-MS and GC × GC-MS: sex differences and host-plant effect. — *Sci. Rep.* **10**: 3092, 13 pp.

Ingram C. 1959: The importance of juvenile cannibalism in the breeding biology of certain birds of prey. — *Auk* **76**: 218–226.

Javidpour J., Molinero J., Ramírez-Romero E., Roberts P. & Larsen T. 2020: Cannibalism makes invasive comb jelly, *Mnemiopsis leidyi*, resilient to unfavourable conditions. — *Commun. Biol.* **3**: 212, 7 pp.

Johnson J.C., Ivy T.M. & Sakaluk S.K. 1999: Female remating propensity contingent on sexual cannibalism in sagebrush crickets, *Cyphoderris strepitans:* a mechanism of cryptic female choice. — *Behav. Ecol.* **10**: 227–233.

Jones P.L. & Agrawal A.A. 2017: Learning in insect pollinators and herbivores. — *Annu. Rev. Entomol.* **62**: 53–71.

Kim K.W., Roland C. & Horel A. 2000: Functional value of matriphagy in the spider *Amaurobius ferox.* — *Ethology* **106**: 729–742.

Lesne P., Trabalon M. & Jeanson R. 2016: Cannibalism in spiderlings is not only about starvation. — *Behav. Ecol. Sociobiol.* **70**: 1669–1678.

Liu X., Xia J., Pang H. & Yue G. 2017: Who eats whom, when and why? Juvenile cannibalism in fish Asian seabass. — *Aquacult. Fish.* **2**: 1–9.

Martinović M., Dender D., Kulijer D. & Koren T. 2023: New records of true bugs (Heteroptera: Lygaeidae) for the fauna of Croatia and Bosnia and Herzegovina — *Entomol. Croat.* **22**: 37–43.

Mathews J.D. 2008: The changing face of kuru: A personal perspective. — *Philos. Trans. R. Soc. (B)* **363**: 3679–3684.

Mayntz D. & Toft S. 2006: Nutritional value of cannibalism and the role of starvation and nutrient imbalance for cannibalistic tendencies in a generalist predator. — *J. Anim. Ecol.* **75**: 288–297.

Michaud J.P. 2003: A comparative study of larval cannibalism in three species of ladybird. — *Ecol. Entomol.* **28**: 92–101.

Mock D.W. & Parker G.A. 1997: *The Evolution of Sibling Rivalry.* Oxford University Press, Oxford, 464 pp.

Omkar, Pervez A. & Gupta A.K. 2007: Sibling cannibalism in aphidophagous ladybirds: Its impact on sex-dependent development and body weight. — *J. Appl. Entomol.* **131**: 81–84.

Perry J.C. & Roitberg B.D. 2005: Games among cannibals: Competition to cannibalize and parent-offspring conflict lead to increased sibling cannibalism. — *J. Evol. Biol.* **18**: 1523–1533.

Pervez A., Chandra S. & Kumar R. 2021: Effect of dietary history on intraguild predation and cannibalism of ladybirds' eggs. — *Int. J. Trop. Insect Sci.* **41**: 2637–2642.

Petersen A., Nielsen K.T., Christensen C.B. & Toft S. 2010: The advantage of starving: Success in cannibalistic encounters among wolf spiders. — *Behav. Ecol.* **21**: 1112–1117.

Pfennig D.W. 1997: Kinship and cannibalism. — *BioScience* **47**: 667–675.

Pokharel P., Steppuhn A. & Petschenka G. 2021: Dietary cardenolides enhance growth and change the direction of the fecundity-longevity trade-off in milkweed bugs (Heteroptera: Lygaeinae). — *Ecol. Evol.* **11**: 18042–18054.

R Core Team 2025: *R: A Language Environment for Statistical Computing. Version 4.5.1.* R Foundation for Statistical Computing, Vienna.

Richardson M.L., Mitchell R.F., Reagel P.F. & Hanks L.M. 2010: Causes and consequences of cannibalism in noncarnivorous insects. — *Annu. Rev. Entomol.* **55**: 39–53.

Roberts J.A., Taylor P.W. & Uetz G.W. 2003: Kinship and food availability influence cannibalism tendency in early-instar wolf spiders (Araneae: Lycosidae). — *Behav. Ecol. Sociobiol.* **54**: 416–422.

Root R.B. 1986: The life of a californian population of the facultative milkweed bug, *Lygaeus kalmii* (Heteroptera: Lygaeidae). — *Proc. Entomol. Soc. Wash.* **88**: 201–214.

Root R.B. & Chaplin S.J. 1976: The life-styles of tropical milkweed bugs, *Oncopeltus* (Hemiptera: Lygaeidae) utilizing the same hosts. — *Ecology* **57**: 132–140.

Schausberger P. 2005: The predatory mite *Phytoseiulus persimilis* manipulates imprinting among offspring through egg placement. — *Behav. Ecol. Sociobiol.* **58**: 53–59.

Schausberger P. & Hoffmann D. 2008: Maternal manipulation of hatching asynchrony limits sibling cannibalism in the predatory mite *Phytoseiulus persimilis.* — *J. Anim. Ecol.* **77**: 1109–1114.

Schausberger P. & Peneder S. 2017: Non-associative versus associative learning by foraging predatory mites. — *BMC Ecol.* **17**: 2, 8 pp.

Shuker D.M., Currie N., Hoole T. & Burdfield-Steel E.R. 2015: The extent and costs of reproductive interference among four species of true bug. — *Popul. Ecol.* **57**: 321–331.

Solbreck C. & Sillén-Tullberg B. 1990: Population dynamics of a seed feeding bug, *Lygaeus equestris*. 1. Habitat patch structure and spatial dynamics. — *Oikos* **58**: 199–209.

Soulsby D. 2013: *Animal Cannibalism: The Dark Side of Evolution*. 5m Publishing, Sheffield, 585 pp.

Sweet II M.H. 2000: Seed and chinch bugs (Lygaeoidea). In Schaefer C.W. & Panizzi A.R. (eds): *Heteroptera of Economic Importance*. CRC Press, Boca Raton, pp. 143–264.

Van Allen B.G., Dillemuth F.P., Flick A.J., Faldyn M.J., Clark D.R., Rudolf V.H.W. & Elderd B.D. 2017: Cannibalism and infectious disease: Friends or foes? — *Am. Nat.* **190**: 299–312.

Wilder S.M., Rypstra A.L. & Elgar M.A. 2009: The importance of ecological and phylogenetic conditions for the occurrence and frequency of sexual cannibalism. — *Annu. Rev. Ecol. Evol. Syst.* **40**: 21–39.

Wu S., Zeng W., Deng W., Li M., Hu W., Cai H., Li Y., Xie P., Tan L. & Zhou Z. 2021: Egg cannibalism varies with sex, reproductive status, and egg and nymph ages in *Arma custos* (Hemiptera: Asopinae). — *Front. Ecol. Evol.* **9**: 705318, 9 pp.

Yadav T., Omkar & Mishra G. 2023: Dietary conditioning on aphids and conspecific eggs in the ladybird *Menochilus sexmaculatus* Fabricius influences cannibalistic food choices in subsequent generations. — *J. Zool.* **321**: 90–98.

Received October 9, 2025; revised and accepted April 20, 2026

Table S1. Sample sizes for Experiment 1.

Developmental stage	*Lygaeus creticus*	*Lygaeus equestris*	*Lygaeus simulans*	*Spilostethus pandurus*
1	17	17	17	15
2	13	16	17	18
3	15	17	14	16
4	14	16	16	18
5	16	15	13	16
Adult	28	29	31	30