# Life stage affects prey use with fitness consequences in a zoophytophagous mirid bug

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# Abstract

Omnivorous insects make foraging decisions between plant and prey resources depending on their accessibility, availability, and nutritional value. This shapes the stability and complexity of foodwebs, but also pest control services in agroecosystems. The mirid bug *Lygus pratensis* is a common cotton pest in China, but it also feeds on a variety of prey species. However, little is known about how different types of available resources affect its fitness and foraging behaviour. In laboratory experiments, we measured the fitness (survival, longevity and fecundity) of *L. pratensis* fed with bean pod only, bean + *Aphis gossypii* nymphs, or bean + *Helicoverpa armigera* eggs, and we also conducted focal observations of its foraging behaviour when provided the latter two. Adding *H. armigera* to its diet increased its fitness (both survival and fecundity), while adding *A. gossypii* was marginally detrimental. The different diets did not affect the time spent walking (searching for food resources) or preying, but significantly affected the time spent sapping bean tissue depending on *L. pratensis* life stage. Nymphs spent more time sapping plant when provided with *H. armigera* than *A. gossypii* (possibly through higher efficiency of handling prey). In addition, adults spent less time sapping plant than did nymphs (possibly through good efficiency of handling *A. gossypii* mobile prey and due to higher protein requirements). This special case of life-history omnivory highlights the complexity of natural foodwebs, where a major pest at the juvenile stage may reduce pest damage by preying on other pests species at the adult stage.

# 1. Introduction

Omnivores are species that can feed on two or more trophic levels, e.g. omnivorous insects may prey on other insects and feed on plants (Jaworski et al., 2013; Pappas *et al.*, 2018; Pérez-Hedo et al., 2021). Foraging for prey or feeding on the plant is largely context-dependent, depending on the availability and type of resources, and the life stage of the omnivore itself (Coll & Guershon, 2002; Han et al., 2020). Such a foraging pattern is common in insects, and is partly responsible for the observed complexity and high connectedness of plant-insect food webs (Sinia et al., 2004; Thompson et al., 2007; Han et al., 2015a, 2020).

Miridae are one of the major families of omnivorous insects (Thompson et al., 2007). For optimal fitness, such omnivorous predators acquire complementary nutrients and energy from host plants and animals, which greatly differ in nutritional value and chemical composition (Eubanks & Denno, 2000; Coll & Guershon, 2002; Magalhaes et al., 2005; Sabelis & van Rijn, 2006; Lundgren et al., 2009; Desneux & O'Neil, 2008). They attack various insect pests that cause significant damage to agricultural and/or horticultural crops, for example, whiteflies, thrips, aphids, and lepidopteran pests and are widely used as biocontrol agents (Chailleux et al., 2013; Jaworski et al., 2015; Thomine et al., 2020). For instance, *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) has been widely used as a biocontrol agent for the management of whiteflies and lepidopteran pests in greenhouses in Europe (Chailleux et al., 2013; Han et al., 2015a, 2015b; Han et al., 2019). The high availability of plant material in a habitat also conditions the switching from prey to plant feeding, perhaps irrespective of prey density (Gillespie et al., 2010; Vankosky &

Vanlaerhoven, 2015). However, most Miridae species are predatory throughout their life stage no matter whether plant food is available (Kaplan & Thaler, 2011).

*Lygus pratensis* (L.) (Hemiptera: Miridae) is a common pest species in cotton crops in Xinjiang, northwest China (Lu et al., 2008, 2010; Lu & Wu, 2011). It also infests many other crops including alfalfa, Chinese date, grape, and pear (Yang et al., 2004; Su & Yuan, 2012). It is a sap-sucking insect and both juveniles and adults can extract nutrients from plants by attacking various plant tender parts, causing plant stunting, abscission of squares and bolls (in cotton), and fruit malformation resulting in significant quality and yield losses (Wang et al., 1996). However, it can also be beneficial to crops due to its pest control capacity. It attacks other insect pests, such as eggs of the cotton bollworm *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae), and cotton aphids *Aphis gossypii* Glover (Hemiptera: Aphididae), the two main cotton pests in China (Wu et al., 2005; Yao et al., 2016). A better understanding of the feeding behaviour of *L. pratensis* is necessary to assess its potential as biocontrol agent versus as a crop pest in agroecosystems.

One important characteristic for predators to select prey is prey mobility (Maselou et al., 2018). As primary insect pests in cotton, *H. armigera* and *A. gossypii* (Lu et al., 2012; Lu et al., 2022) are preyed upon by *L. pratensis* similarly to other zoophytophagous mirid bugs (Alvarado et al., 1997; Li et al., 2020). While *H. armigera* eggs are immobile, *A. gossypii* nymphs are mobile and able to defend. Besides, the nutritional value of *H. armigera* eggs may be higher than that of *A. gossypii* nymphs (higher lipid and protein content), and this could increase the preference and fitness of *L. pratensis* to feed on *H. armigera* eggs. Indeed, many studies have shown that Lepidopteran eggs are high in lipids and proteins and may thus best satisfy nutritional needs: generalist insect predators that fed on Lepidopteran eggs had higher survival, a shorter development time, and a higher fecundity than those fed on other prey species (Siddique & Chapman, 1987; Lumbierres et al., 2021; Ren et al., 2022). Here, we tested two hypotheses: (i) *L. pratensis* feeding on *H. armigera* eggs rather than *A. gossypii* nymphs may increase *L. pratensis* fitness; (ii) the feeding behaviour (predominantly plant feeding versus prey feeding) of *L. pratensis* depends on life stage (juvenile versus adult) and on the prey type.

## 2. Materials And Methods

## 2.1. Study organisms

*Lygus pratensis* was originally collected from fields of alfafa *Medicago sativa* (Fabales: Fabaceae) by sweep-netting in Shihezi (44°27'N, 85°94'E), Xinjiang Uyghur Autonomous Region of China, in August 2017. The species was identified following procedures used in previous studies (Lu et al., 2008; Liang et al., 2013). It was reared in plastic rearing containers (20 × 13 × 8 cm) under controlled laboratory conditions (25 ± 2°C, 60 ± 5% RH and 16L: 8D). The food resources provided were green bean pods *Phaseolus vulgaris* L. (Fabales: Fabaceae) commercially available in Shihezi, Xinjiang, China, and a 10% sucrose solution. Green bean pods were used as oviposition substrate and were renewed every other day. Bean pods with eggs were moved to individual petri dishes, lined with filter paper, and kept in the

incubator under the same climatic conditions. *Lygus pratensis* individuals of the first generation were used for the experiment. Aphids *A. gossypii* were collected from a cotton field in Shihezi, Xinjiang, China, while *H. armigera* adults were collected by light traps on the campus of Shihezi University. Both were reared on cotton seedlings (*Gossypium hirsutum* L.) in separate cages under the same climatic conditions as above.

## 2.2. Fitness traits of *L. pratensis*

The methodology was similar to that described by Lu et al. (2008). *Lygus pratensis* individual females were held for 24 h in rearing boxes for oviposition (with fresh green beans as the oviposition substrate). Newly-hatched *L. pratensis* nymphs (within 12 h) were placed in microcosms made of a petri dish covered by an upside-down plastic cup with ventilation on the top (Jaworski et al., 2013). The petri dish was lined up with absorbent cotton, and a bean pod was provided on a pin through the cup wall. The food treatment was either: (a) one fresh bean pod only; (b) one fresh bean pod and 50 *A. gossypii* nymphs; or (c) one fresh bean pod and 50 *H. armigera* eggs. The exact number of prey was deposited in the microcosm using a fine brush to not damage them. 70 replicates of each treatment were prepared. Bean pods (mass ~ 3 g; length ~ 4.5 cm) were previously soaked in a 0.5% sodium hypochlorite solution for 10 min to remove any pesticide residue and then rinsed with water and dried with absorbent paper. Bean pods and prey were replaced every day to ensure enough fresh food was available for the development of *L. pratensis*. Each *L. pratensis* nymph was checked daily to record emergence of the next instar, until they reached adulthood or died. The emerged adults were sexed and paired (female: male ratio 1: 1) before being placed in the same microcosm (N = 30). After mating, the females lay eggs in the oblique section of the bean pod, and eggs can be easily observed under the microscope. Laid eggs were counted every day until the female died to calculate fecundity. Adult longevity was calculated as the total number of days before death occurred.

## 2.3. Foraging behaviour of *L. pratensis*

Focal observations of the foraging behaviour of *L. pratensis* were performed under the same laboratory conditions as above. Foraging behaviour is the process by which an animal searches for and feeds on food. It involves a series of activities including orientation, prey/host plant location, and prey handling/plant consumption (Schone, 2014). We used five behavioural categories (after Rosenheim et al., 2004): (1) resting (insect staying still); (2) grooming (grooming antenna, stylet or wings with forefoot); (3) walking (moving but no contact of mouthparts with plant or prey); (4) sapping plant (inserting stylet into plant material for more than 5 s and with the head moving up and down); (5) preying (prey probing: stylet in contact with prey, or prey feeding: stylet inserted into prey for more than 5 s). Behaviours 3–5 are part of the foraging activity. After being starved for 24 h and for each diet treatment, 25 nymphs and 20 virgin adults including 10 females and 10 males (sex ratio 1:1) were individually placed in a petri dish (diameter: 7.0 cm). The diet treatments were: (a) a fresh bean pod and 50 3rd -4th *A. gossypii* nymphs or (b) a fresh bean pod and 50 *H. armigera* eggs. Each individual was observed continuously for 20 min under a stereomicroscope (Nikon, at 3.0× magnification with a 10× ocular lens) and the time spent on each of the five behaviours was recorded. All focal observations were conducted by the same observer

and between 10:00 and 20:00 during daylight hours (following Rosenheim et al., 2004). For each individual, the total time spent on each behaviour was calculated.

## 2.4. Statistical analyses

All analyses were performed using the R software (R Core Team, 2022). When using linear models and generalised linear models (GLMs), the absence of residual heteroscedasticity and overdispersion was verified in the best model using the functions 'simulateResiduals()' and 'testDispersion' (library 'DHARMa'; Hartig, 2022). If fixed effects were significant, biologically relevant comparisons of means between groups were performed with a Tukey test for linear models with a single fixed effect (function 'TukeyHSD', library 'stats'; R Core Team, 2022) and otherwise with the 'emmeans' function (library 'emmeans'; Lenth, 2019).

Survival rate as a function of diet was analysed using a Cox proportional hazards regression model with diet as fixed effect on (i) the whole life span, and (ii) juvenile stage (survival until adult emergence; function 'coxph', library 'survival'; Therneau, 2022), and using the 'relevel' function (library 'stat', R Core Team, 2022) to compare pairs of treatments. Survival curves (Fig. 1) were created with the 'survfit' function (library 'survival') to model the fit, and the 'ggsurvplot' function to plot the fit (library 'survminer'; Kassambara et al., 2021). We also assessed how diet affected the proportion of nymphs reaching adulthood using a GLM with diet as fixed effect and a binomial distribution (function 'glm', library 'stats'; R Core Team, 2022). Then, we assessed how diet affected the longevity of adults and the fecundity of females using linear models and an ANOVA with diet as fixed effect.

We assessed the effect of diet and life stage (nymphs vs. adults) and the interaction between these two factors on the foraging activity budget (time spent walking, sapping plant or preying) of *L. pratensis* using independent regressions and adjusting *P*-values *a posteriori* (Huang, 2020) with the Benjamin & Hochberg (1995) correction to account for data non-independence (function 'p.adjust; library 'stats'; R Core Team, 2022). We used a linear model for sapping plant and GLMs with a negative binomial error distribution for the other two activities to account for data overdispersion (function 'glm.nb' library 'MASS'; Venables & Ripley, 2002). The significance of fixed effects for each test was estimated through a stepwise regressive type-II model comparison with an ANOVA.

## 3. Results

## 3.1. Effects of diet on fitness: survival, longevity, and fecundity

The survival rate of *L. pratensis* over their entire life span was affected by their diet, although survival on a bean + *A. gossypii* diet was only marginally lower than survival on a bean + *H. armigera* eggs diet (Table 1; Fig. 1). However, differences were stronger during juvenile development (until day 18–25). Survival was marginally higher on a bean-only diet than a bean + *A. gossypii* diet, but survival was significantly higher on a bean + *H. armigera* eggs diet than on the two other diets. This resulted in a

significant effect of diet on the proportion of nymphs reaching the adult stage (Dev = 23.26, df = 2, $P <$ 0.001; Fig. 2A). Significantly more nymphs reached the adult stage when reared on a bean + *H. armigera* eggs diet than on a bean-only diet or a bean + *A. gossypii* diet (Table 2). However, *L. pratensis*' diet did not significantly affect the longevity of adults ($F_{2,143}$ = 2.39, $P$ = 0.095; Fig. 2B). Finally, female fecundity was significantly affected by diet ($F_{2,97}$ = 9.10, $P <$ 0.001; Table 2; Fig. 2C), due to a two times and 1.4 times higher fecundity on a bean + *H. armigera* eggs diet than on a bean-only diet and on a bean + *A. gossypii* diet, respectively.

Table 1

Effect of diet on survival rate as a function of life span (adult vs. juvenile). Significant effects after *P*-value correction for multiple testing are shown in bold, and if they are significant, comparisons of means between groups are shown. 'AG': bean + *A. gossypii* diet; 'HA': bean + *H. armigera* eggs diet.

| Fixed effect: diet | LR | d.f. | P | Adjusted P |
|---|---|---|---|---|
| Entire life span | 11.4 | 2 | 0.0033 ** | **0.0033 **** |
| Juvenile life stage | 30.0 | 2 | < 0.001 *** | **< 0.001 **** |
| Comparisons of survival between food diets | Coefficient ± SE | P | | Adjusted P |
| *Entire life span* | 0.213 ± 0.127 | 0.095 | | 0.095 |
| bean vs. bean + AG | -0.290 ± 0.145 | 0.045 * | | 0.089 |
| bean vs. bean + HA | -0.363 ± 0.150 | 0.015 * | | 0.062 |
| bean + AG vs. bean + HA | 0.615 ± 0.160 | < 0.001 *** | | **< 0.001 **** |
| *Juvenile life stage* | -0.513 ± 0.230 | 0.026 * | | 0.077 |
| bean vs. bean + AG | -1.128 ± 0.230 | < 0.001 *** | | **< 0.001 **** |
| bean vs. bean + HA | | | | |
| bean + AG vs. bean + HA | | | | |
| **: *P* < 0.01; ***: *P* < 0.001. | | | | |

Table 2

Comparison of means between diets for the proportion of nymphs reaching the adult stage (emmeans test) and for female fecundity (Tukey test). Significant differences are shown in bold.

| emmeans test | estimate ± SE (on log scale) | P |
|---|---|---|
| *Proportion of nymphs reaching the adult stage* | | |
| bean + AG − bean | -0.559 ± 0.264 | 0.087 |
| bean + HA − bean | 0.928 ± 0.298 | **0.0053 \*\*** |
| bean + HA − bean + AG | 1.487 ± 0.319 | **< 0.001 \*\*\*** |
| **Tukey test** | **Difference [95CI]** | |
| *Fecundity* | | |
| bean + AG − bean | 41.0 [ -30.0; 112] | 0.22 |
| bean + HA − bean | 95.6 [29.8; 161] | **< 0.001 \*\*\*** |
| bean + HA − bean + AG | 54.6 [-16.4; 126] | 0.13 |
| \*\*: *P*< 0.01; \*\*\*: *P*< 0.001. | | |

## 3.2. Foraging behaviour

The time spent walking and preying was not significantly affected by the diet nor life stage and neither by the interaction between the two (Table 3; Fig. 3). However, the diet in interaction with life stage significantly affected the time spent sapping plant: nymphs spent 1.5 times more time sapping plants when provided with a bean + *H. armigera* eggs diet compared to a bean + *A. gossypii* diet, and nymphs spent 1.4 times more time sapping plants than adults in a bean + *H. armigera* diet, but not in a bean + *A. gossypii* diet (mean ± SE: nymphs, bean + *H. armigera*: 820 ± 70; nymphs, bean + *A. gossypii*: 544 ± 90; adults, bean + *H. armigera*: 585 ± 81; adults, bean + *A. gossypii*: 738 ± 69).

Table 3

Effect of diet and life stage on time spent on each foraging behaviour: walking, sapping plant or preying (independent GLMMs). Significant effects after *P*-value correction for multiple testing are shown in bold, and if they are significant, comparisons of means between groups are shown. 'AG': bean and *A. gossypii* diet; 'HA': bean and *H. armigera* eggs diet.

| Fixed effect | LR | d.f. | *P* | Adjusted *P* |
|---|---|---|---|---|
| *Walking* | 2.41 | 1 | 0.12 | 0.12 |
| Diet*life stage | 1.08 | 1 | 0.30 | **0.020 *** |
| Diet | 0.274 | 1 | 0.60 | 0.12 |
| Life stage | 7.67 | 1 | 0.0067 ** | |
| *Sapping plant* | 3.03 | 1 | 0.082 | |
| Diet*life stage | 0.00218 | 1 | 0.96 | |
| *Preying* | 0.130 | 1 | 0.72 | |
| Diet*life stage | | | | |
| Diet | | | | |
| Life stage | | | | |

| Mean comparisons between groups | Estimate ± SE | P | | |
|---|---|---|---|---|
| *Sapping plant (s)* | 153 ± 107 | 0.16 | | |
| Adults: AG − HA | -276 ± 112 | **0.016 *** | | |
| Nymphs: AG − HA | 194 ± 109 | 0.079 | | |
| HA: adults − nymphs | -235 ± 110 | **0.035 *** | | |
| AG: adults − nymphs | | | | |

*: *P* < 0.05; **: *P* < 0.01.

# 4. Discussion

Whether an phytophagous bug is a crop pest may depend on its capacity to feed on prey in relation to lifestage. In this study we investigated how the presence of prey affected the foraging behaviour and fitness of the omnivorous but mostly phytophagous mirid bug *L. pratensis*. We found that feeding on a bean + *H. armigera* eggs diet increased fitness (higher survival and fecundity), while a bean + *A. gossypii* diet had marginally detrimental effects, compared to a bean-only diet. We also found that the foraging behaviour was altered by diet: nymphs spent more time sapping plant on a bean + *H. armigera* diet compared to a bean + *A. gossypii* diet, and they also spent more time than adults sapping plants on a bean + *H. armigera* diet.

Supplementing *H. armigera* eggs in addition to green bean pods enhanced *L. pratensis* survival and fecundity (but not longevity). Adding protein-rich eggs to a plant-based diet has been shown to increase fitness in other predatory bugs (Siddique & Chapman, 1987; Urbaneja et al., 2005; Jaworski et al., 2015; Maselou et al., 2018; Ren et al., 2022). This is evidence that omnivorous mirid bugs may need prey as part of their diet to achieve optimal reproduction (Han et al., 2015a). Here, we observed that *L. pratensis* was attracted to and very often preyed on *H. armigera* eggs when provided in food mixtures.

In contrast, the supplement of *A. gossypii* aphids to a bean diet had marginally detrimental effects on *L. pratensis* fitness. A lower fitness on a bean + *A. gossypii* diet compared to a bean + *H. armigera* diet could be due to the lower nutritional quality of *A. gossypii* nymphs compared *H. armigera* eggs) but this does not explain why supplementing *A. gossypii* was marginally detrimental to *L. pratensis*. One reason could be the difficulty to attack prey, leading on significant time and energy loss and therefore poorer fitness, as most predators, both mammals or arthropods, select food resources based simultaneously on availability, accessibility (e.g., prey size), and nutritional quality (Woodward & Hildrew, 2002). Third and 4th instar aphid nymphs were used in the experiments and their individual sizes were larger than those of *L. pratensis* juveniles. In addition, aphids show various mechanisms to defend themselves against predatory attacks (e.g. see Desneux et al., 2009; Luo et al., 2022). Rosenheim et al. (2004) observed that most often, *Lygus hesperus* ignored aphid prey or retreated upon contact. By contrast, *L. pratensis* nymphs provided with bean + *H. armigera* eggs could have better optimized their foraging activity by quickly feeding on *H. armigera* eggs and therefore spending more time sapping bean tissue.

Conversely to *L. pratensis* nymphs, adults did not spend more time sapping bean tissue when *H. armigera* eggs were provided compared to when *A. gossypii* nymphs were provided. This could be because they were more efficient at attacking *A. gossypii* than nymphs were, and therefore could have been able to feed on prey and plant tissue at equivalent rates no matter what prey type was provided. It is likely that handling *H. armigera* eggs was not more difficult for *L. pratensis* nymphs than adults since egg prey are immobile. Also in average, *L. pratensis* adults spent less time sapping bean tissue than did *L. pratensis* nymphs. This was in part compensated (although not significantly) by spending more time preying. This may be related to a higher protein requirement by the time of reaching sexual maturity, especially under a suboptimal diet during the juvenile stage (Barrett et al., 2009). Bean tissue-mediated indirect interactions between *L. pratensis* and *A. gossypii*, both feeding on bean tissue, were likely minor in explaining *L. pratensis* behavioural changes here, since plant defences in *in vitro* plant parts are lower (Heil & Ton, 2009).

In conclusion, the fitness and foraging behaviour of *L. pratensis* varied with the diet provided: *L. pratensis* nymphs were efficient at preying on immobile *H. armigera* eggs, which increased their time spent feeding on bean tissue, while *L. pratensis* adults spent similar time feeding on plant tissue versus prey no matter the prey type. This suggests life-history omnivory, that is *L. pratensis* incorporate more prey content in their diet once they reached adulthood – a phenomenon that was found to increase the stability of food webs (Kratina et al., 2012). With regards to the pest status of *L. pratensis*, our study suggests that mostly

juveniles are crop pests since they spend more time than adults feeding on plant tissue. While adults still considerably feed on plant tissue, they may also reduce plant damage caused by alternative pest species.

# Declarations

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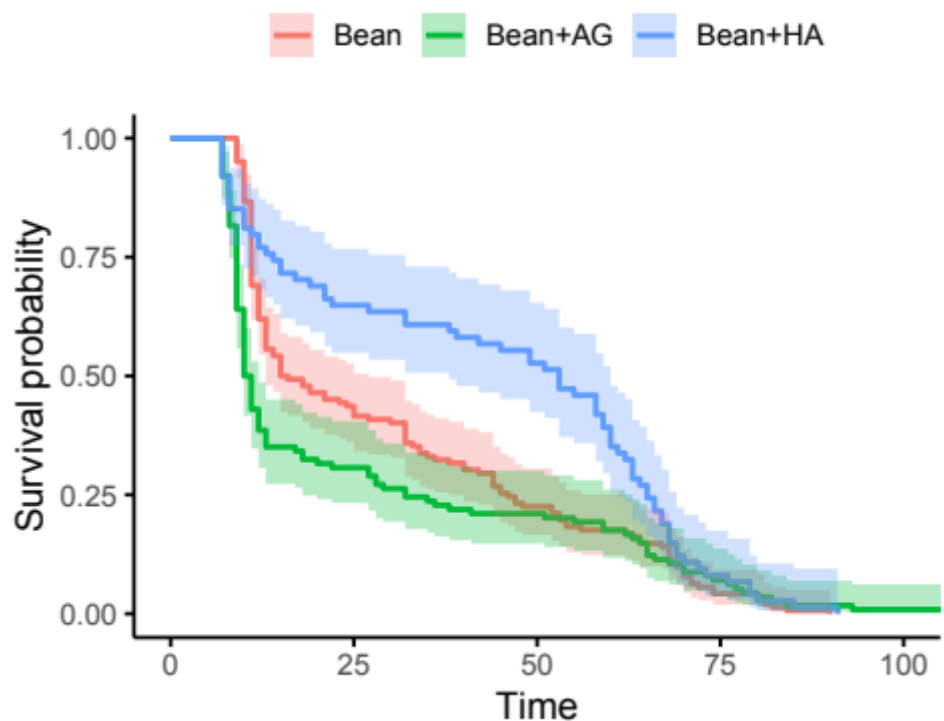
# Figures



Figure 1

Survival rate of *L. pratensis* through time reared on three different diet ('Bean': bean pod only; 'Bean+AG': bean pod + *A. gossypii*; 'Bean+HA': bean pod + *H. armigera* eggs). Shaded areas show the 95 % confidence intervals.
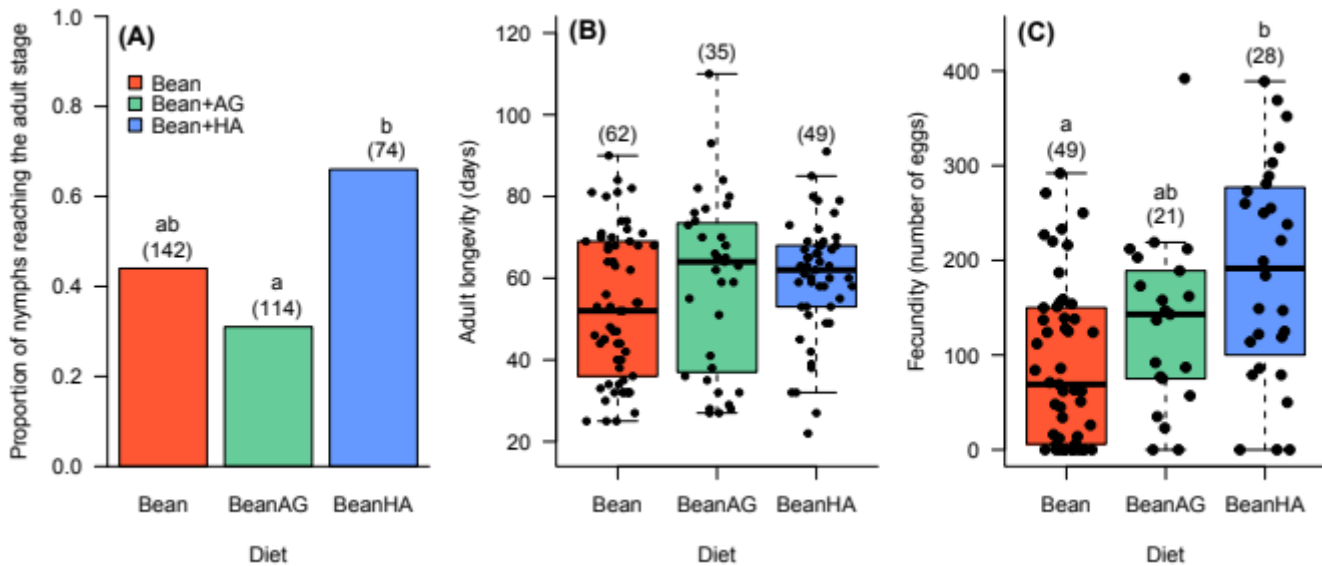
**Figure 2**

Proportion of nymphs reaching adult stage (A); Adult longevity (boxplot; B); and female fecundity (boxplot; C) as a function of diet. 'Bean': bean-only diet; 'Bean+AG': bean + *A. gossypii* diet; 'Bean+HA': bean + *H. armigera* diet. Numbers in parentheses show sampling sizes for each group. Significant differences between diets are shown with different letters above bars (mean comparisons; Table 2). The scale in (B) starts from the earliest observed emergence time of adults (day 18).
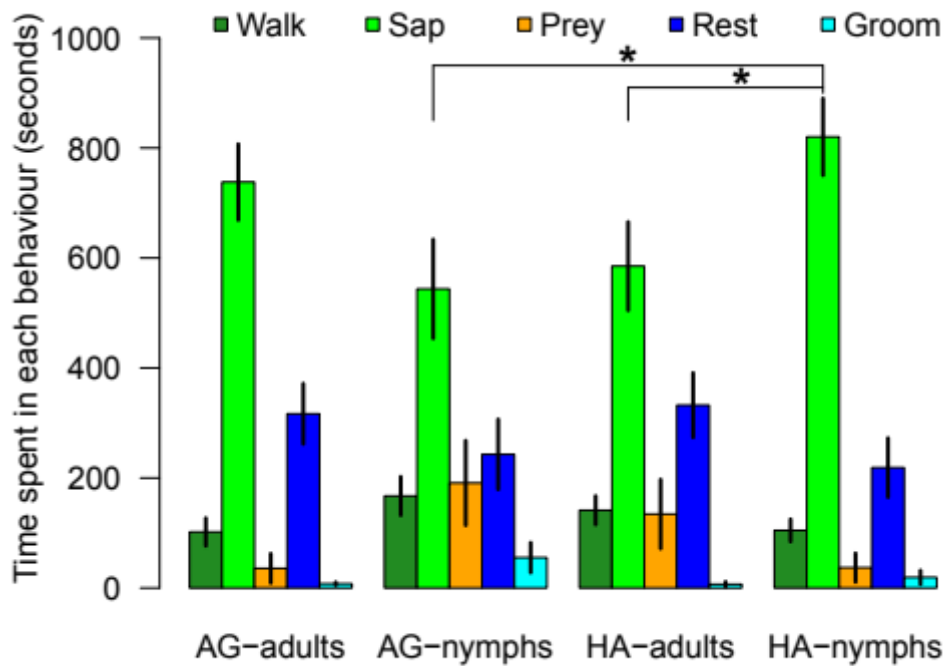


**Figure 3**

Mean (± SE) time spent on five different behaviours of *L. pratensis* nymphs and adults feeding on bean and *A. gossypii* (AG) or bean and *H. armigera* eggs (HA) for 20 min. 'Walk': walking; 'Sap': sapping plant; 'Prey', preying; 'Rest': resting; 'Groom': grooming. Significant differences between treatments for the three foraging behaviours (walking, sapping plant or preying) are shown with '*' (see Table 1).

## Supplementary Files

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