

## Research Paper

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# Host age preference and biology of *Coccygidium luteum* (Hymenoptera: Braconidae), a larval parasitoid of the fall armyworm

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## Abstract

*Coccygidium luteum* (Hymenoptera: Braconidae), a solitary larval parasitoid, is associated with the fall armyworm (FAW), in Africa. However, there is very limited information on reproductive biology, and other biological parameters that influence its life strategies. We conducted laboratory experiments to gain new insights into the biology of *C. luteum* reared on FAW as the host. Host age preference, reproductive biology, lifetime fecundity, life cycle, and adult longevity were studied under laboratory conditions of  $28 \pm 1^\circ\text{C}$  and  $70 \pm 3\%$  relative humidity. This study revealed that *C. luteum* prefer early (1st–3rd) instars of FAW for oviposition. The maximum parasitism rate was 80% at second instar larvae. A mean pre-oviposition period of  $0.38 \pm 0.51$  days, oviposition period of  $5.13 \pm 0.64$  days, and no post-oviposition period were observed. The mean lifetime parasitism rate of FAW larvae by female *C. luteum* was  $49 \pm 24$ . Longevity of unmated *C. luteum* was  $14.44 \pm 1.43$  days for males and  $12.83 \pm 1.12$  days for females. Mated ovipositing females lived for 7 days. Mean female and male progenies per adult female *C. luteum* was  $28.11 \pm 8.18$  and  $39.89 \pm 4.76$  respectively, with an overall sex ratio of  $1.42$  at  $28 \pm 1^\circ\text{C}$  using second instar larvae. Total life cycle from oviposition to adult emergence was  $23 \pm 1$  days. This study provides the basic information about *C. luteum* that could be utilised for mass rearing of this parasitoid under an augmentative biological control of FAW programme.

## Introduction

The fall armyworm (FAW) (*Spodoptera frugiperda*: Lepidoptera: Noctuidae), which is native to the tropical Americas, was first reported in Africa in 2016 (Goergen *et al.*, 2016) and has since spread to Asia and Australia (Qi *et al.*, 2021; Srikanth *et al.*, 2018). FAW is a devastating polyphagous pest with over 350 host plant species but is mostly found on maize (Montezano *et al.*, 2018). Meanwhile, maize is the main staple food crop for over 300 million Africans and a major source of livelihood and nutritional security across the world (Shiferaw *et al.*, 2011). In the absence of any control measure, FAW is estimated to cause over 80% yield loss (Abrahams *et al.*, 2017a). In Ghana, the national yield loss due to FAW was estimated to be 26.6% in 2017 valued at US\$ 177 m (Abrahams *et al.*, 2017a). The distribution of pesticides by many African countries for FAW control has led to their acceptance by farmers as the primary means of FAW management (Kansiime *et al.*, 2019; Tambo *et al.*, 2020). However, the likely misuse of these hazardous pesticides poses human health and environmental threats and could lead to insecticide resistance in FAW (Abraham *et al.*, 2018; Ihara *et al.*, 2017; Ullah and Shad, 2017). Boaventura *et al.* (2020) showed high frequency of targeted site mutations conferring insecticide resistance in FAW in Kenya. Recent reports indicate that the application of high doses of insecticides to control FAW has resulted in resurgence of insects in maize farms (Kumar *et al.*, 2022). These suggest that biological control could be a promising alternative to chemical control.

Moreover, biological control of FAW has been considered more sustainable to chemical control because it is environmentally friendly, improves food safety by eliminating chances of pesticides residue, and prevents resistance development (Abbas *et al.*, 2022). To find a sustainable management option for FAW in Africa, scientists across the continent initiated the search for locally occurring natural enemies adapted to the pest, for possible biological control. These studies have identified several predators, parasitoids and a few entomopathogens attacking the pest in the field (Agboyi *et al.*, 2020; Ahissou *et al.*, 2021a). The majority of parasitoid species reported on FAW in Africa are larval parasitoids, including *Coccygidium luteum*

(Brullé) (Hymenoptera: Braconidae) (Agboyi et al., 2019; Ahissou et al., 2021a; Durocher-Granger et al., 2021; Otim et al., 2021). In Ghana, *C. luteum* was found in all agro-ecological zones attacking FAW and it was the most dominant parasitoid species found (Agboyi et al., 2020). Conversely, in Kenya and Tanzania, field parasitism rate *C. luteum* was only 9% (Sisay et al., 2018). *Coccygidium luteum* belongs to the sub-family Agathidinae with more than 45 genera (Sharkey and Chapman, 2017). It is one of the 26 species of the genus *Coccygidium*, which consists of a group of solitary koinobiont larval endoparasitoids of Lepidoptera (Ghramh, 2011). In its distribution range, *C. luteum* is a parasitoid of other Noctuidae. It is the most widely reported larval parasitoid associated with FAW in Africa and has been reported in several African countries including Ghana and Benin (Agboyi et al., 2020), Cameroon (Abang et al., 2021), Uganda (Otim et al., 2021), Kenya, Ethiopia and Tanzania (Sisay et al., 2018), Burkina Faso (Ahissou et al., 2021a), and Mozambique (Caniço et al., 2020). In Ghana, *C. luteum* is one of ten parasitoid species attacking FAW (Agboyi et al., 2020). To confirm its identity, morphological and molecular identification were conducted by the diagnostic services laboratory of the Centre for Agriculture and Biosciences International (CABI). Voucher specimens were deposited at GenBank (<https://www.ncbi.nlm.nih.gov/nuccore/MN900728,MN900739,MN900741>).

Until the invasion of the FAW, the biology and ecology of *C. luteum* were not comprehensively studied. There is very limited information on the main hosts of this parasitoid in Africa and its potential as biological control agent against important lepidopteran pests on the continent. Currently, there is no research on host age preference, parasitism rate, sex ratio, pre-oviposition period, longevity, and effect of superparasitism on this parasitoid thereby hindering its possible use in biological control of FAW. Recently, Agboyi et al. (2019) reported a 19% field parasitism rate of FAW by *C. luteum* and have also demonstrated that the amount of maize leaves consumed by FAW larvae parasitised by *C. luteum* declined by 89% compared to unparasitised larvae. These studies have demonstrated a high potential of *C. luteum* as an agent for augmentative biological control of FAW in Africa. However, it could be possible to optimise the level of parasitism if the biology of the parasitoid is better understood. Indeed, understanding the reproductive biology of parasitoids and factors influencing them is a prerequisite for assessing their biological control potential and their efficient use in biological control programmes. For instance, it has been established that percent parasitism of *Diaprepes abbreviatus* eggs by *Ceratogramma etiennei* decreases as eggs mature (Amalin et al., 2005). Also, it is known that younger *Trichogramma euproctidis* females parasitised more *Ephesia kuehniella* eggs than older ones (Tabebordbar et al., 2022). It is unknown if similar relationships exist between the larvae of FAW and their parasitoids because earlier studies did not focus much on the biology and host age preference of *C. luteum*. It is therefore imperative to study these. In this paper, we provide a detailed report on the host age preference and reproductive biology of *C. luteum*.

## Materials and methods

### Laboratory colony of *Coccygidium luteum* and its host FAW

Rearing of the parasitoid, *C. luteum*, and its host, FAW, was carried out at the Biological Control Laboratory of the Plant Protection and Regulatory Services Directorate (PPRSD) of the Ministry of Food and Agriculture (MOFA) located in Accra, Ghana. Approximately 500 FAW larvae were collected from infested maize

fields in Somanya in the Eastern Region of Ghana during the major maize growing season in May 2021. For the purpose of this study, the collected FAW larvae were categorised as 'early instars' (1st–3rd instar) and late instars (4th–6th instar) following the FAW larval identification guide <https://www.agric.wa.gov.au/sites/gateway/files/Fall%20armyworm%20larval%20identification%20guide%20DPIRD.pdf> (Capinera, 2020) and kept in transparent plastic bowls (18.5 × 12.5 × 4.5 cm; Unipak Ltd, Accra, Ghana). They were provided with maize leaves as feed and transported to the laboratory. In the laboratory, the larvae were separated individually into 80 ml transparent plastic cups (Everpack Ltd, Accra, Ghana) with perforated lids for aeration and provided with fresh young maize leaves as feed. Monitoring of the larvae and changing of the leaves were done every other day until FAW or parasitoids pupated. FAW larvae that were parasitised by *C. luteum* yielded parasitoid cocoon. Both FAW pupae and parasitoid cocoon were observed daily for adult emergence. After emergence, the adults of *C. luteum* were used to establish a laboratory culture of the parasitoid. The FAW moths obtained from pupated non-parasitised larvae were used to establish a host culture in 34 × 30 cm locally manufactured oviposition cages made from transparent cylindrical plastic buckets. The inner walls of the cages were cleaned regularly using cellulose paper to avoid contamination. The lids of the cages were ventilated, using white polyester material. Additionally, on one side of the cage, an opening measuring 11 × 12 cm was ventilated with white polyester material and a sleeve located at the opposite side. The parasitoid and FAW cultures were kept at 28 ± 1°C and 29 ± 1°C respectively, with relative humidity of 70 ± 5% and photoperiod of L12: D12. All tests were carried out under 28 ± 1°C environmental conditions. FAW moths were fed with 70% honey solution soaked in cotton wool and placed in oviposition cages. The colony of adult *C. luteum* was fed with droplets of 100% honey streaked on the internal walls of the cages and provided with water soaked in cotton wool placed in a sauce cup. The cotton wool soaked with water was replaced daily while honey droplets were monitored and replenished when needed. In all the experiments, larvae were exposed to the female parasitoids for oviposition without feed or maize leaves. This was standardised across all experiment with exposure time of 35 minutes.

### Parasitism bioassay

In the laboratory, both early instar (1st–3rd instar) and late instar (4th–6th) FAW larvae collected from the field were monitored for parasitoid emergence. No *C. luteum* emerged from all late instar (4th–6th) larvae ( $n = 200$ ). Based on this observation, further experiments on parasitism were restricted to early instar (1st–3rd instar) larvae only. To determine the stage among the 1st–3rd instars that is preferred for parasitism by *C. luteum*, a no-choice experiment was conducted. In the no-choice experiment, 25 individuals of FAW larvae of a particular stage were placed in oviposition containers (500 ml PET bottles with aerated caps) ( $n = 9$ ) and exposed to a mate female of *C. luteum* for 35 minutes for parasitism without providing feed or maize leaves. After the 35-minute exposure period, the larvae were placed into aerated cups (80 ml) individually and provided with pieces of fresh young maize leaves as feed. The leaves were changed every other day until pupation. The pupae were maintained under the same experimental conditions and observed regularly until adult emergence in 8–12 days. The number of cocoons and emerged parasitoids observed were counted and recorded. The stages for which no-choice experiments

were conducted were first instar (3-day old larvae), early second instar (4-day old larvae), late second instar (5-day old larvae), and third instar (6-day old larvae).

Prior to the no-choice experiments, pairs (male and female) of *C. luteum* were mated for 24 hours in 50 ml plastic vials covered with cotton wool for aeration. The internal walls of the plastic vials were streaked with droplets of honey and a ball of cotton wool soaked in water in a sauce cup was placed at the bottom of the vial.

### Host age preference

Using the susceptible host ages (3-, 4-, 5-, and 6-day old larvae) which correspond to specific stages of early instar FAW larvae from the no-choice experiment, choice experiments were conducted to determine the preferred age (stage of FAW larval instar) by *C. luteum*. Six combinations of larvae, covering all the susceptible host ages, were used as follows: 3- and 4-day old; 3- and 5-day old; 3- and 6-day old; 4- and 5-day old; 4- and 6-day old; and 5- and 6-day old larvae. Fifteen larvae of each age group making a total of 30 larvae were simultaneously placed in a 500 ml PET bottle as an oviposition cage with an aerated cover, using a camel-hair brush. A single mated *C. luteum* female was introduced into the oviposition cage to oviposit for 35 minutes. Each combination was replicated five times. Parasitised larvae were immediately transferred into 80 ml sauce cups containing tissue paper and fresh maize leaves. The feed was replenished every other day, as previously described, until pupation by non-parasitised larvae or cocoon formation by the parasitised larvae. The positions of the sauce cups were changed every 2 days to account for any environmental variation. The number of parasitoid cocoons from each age group combination was recorded.

### Biology of *Coccysidium luteum*

To determine the maximum number of host larvae that a single *C. luteum* can parasitise in a day, an initial test was conducted by exposing 4-day old host larvae to a pair of (one male and one female) parasitoids *ad libitum*. Immediately after adult parasitoid emergence, 4-day old FAW larvae ( $n = 25$ ) were exposed to a pair of *C. luteum* for parasitism in 500 ml PET bottles ( $10.5 \times 7.5$  cm; Everpack) without maize leaves for 35 minutes. The PET bottles were covered with cotton wool for aeration and 100% honey was streaked on the internal walls as feed for the parasitoid. After the 35 minutes of exposure and observation, the parasitoids were transferred into new oviposition containers and held for the next day. Each day, a new set of 25 four-day old FAW larvae were introduced to the same set of parasitoids for 35 minutes, until the death of the female parasitoid. Any male parasitoid that died before the female was replaced, in case the female required multiple mating to maximise reproduction. The parasitised FAW larvae were placed individually into aerated plastic cups (80 ml) and fed with fresh young maize leaves as earlier described, until pupation or cocoon formation. This was replicated nine times. From the 6th day after parasitism, the parasitised larvae were observed twice daily to ensure accurate recording of developmental parameters. The parameters assessed were pre-oviposition period, oviposition period, post-oviposition period, egg to prepupal duration, pupal duration, sex ratio, number of offspring, and lifetime duration of ovipositing female.

Longevity of non-ovipositing adult *C. luteum* was determined by separating unmated male and female parasitoids immediately

**Table 1.** Parasitism (mean  $\pm$  SD) of different instars of fall armyworm larvae by *Coccysidium luteum* under laboratory conditions for 35 minutes at  $29 \pm 1^\circ\text{C}$

Host age	Parasitism rate of <i>C. luteum</i> (%)
3-day old (1st instar)	70.22 $\pm$ 10.79a
4-day old (early 2nd instar)	80.22 $\pm$ 8.35a
5-day old (late 2nd instar)	57.22 $\pm$ 30.46b
6-day old (3rd instar)	32 $\pm$ 20.89c

Percentage parasitism of different ages of fall armyworm larvae by *C. luteum* expressed as percent of number of emerged parasitoid cocoon over total number of host larvae exposed to the adult parasitoid for oviposition. Means followed same letters are not statistically different at  $P = 0.05$  probability level.

after emergence into 500 ml PET bottles and kept without mating. The parasitoids were provided with water and honey, as previously described and observed daily. The water and honey were replenished, when necessary, until the parasitoids died. The duration from emergence to death was recorded to estimate the longevity. A total of 18 males and 18 females were observed.

### Statistical analysis

All the data were subjected to normality test using Shapiro–Wilk test. Data on the parasitism assay were normally distributed so they were subjected to one-way analysis of variance. Means of the different groups were separated using Student–Newman–Keuls post hoc test at 5% probability threshold. Host age preference data were analysed using a two-sample *t*-test with equal variances while other reproductive parameters such as lifetime parasitism, pre-ovipositing, ovipositing, post-ovipositing duration as well as longevity and duration of developmental stages of *C. luteum* were analysed using descriptive statistics. All the data were analysed using STATA/Standard Edition 17.0.

## Results

### Parasitism assay

The susceptible age of FAW for parasitism by *C. luteum* was studied in a no-choice experiment. *C. luteum* was able to parasitise first instar (3-day old) to third instar (6-day old) larvae of FAW with differences in parasitism among the various instars studied. The mean parasitism was highest in 4-day old larvae compared to other age groups ( $F_{3,35} = 10.4$ ;  $P < 0.001$ ) (Table 1). However, there was no statistically significant difference in parasitism between 3-day old and 4-day old host larvae ( $F_{3,35} = 10.4$ ;  $P < 0.280$ ). Susceptibility of host larvae to *C. luteum* parasitism decreased with increasing host age (Table 1). No parasitism or oviposition occurred when 7-day old larvae were exposed to the parasitoid and thus were excluded from the analysis.

### Host age preference

The preferences of *C. luteum* for different ages of FAW larvae were studied in choice experiments as shown in Table 2. *C. luteum* oviposited in both host ages in all the six combinations. Host age preference by *C. luteum* differed significantly in all the combinations except between 3-day and 4-day old larvae and between 4-day and 5-day old larvae. Significantly, 6-day old (3rd instar) larvae were less parasitised in all the age combinations they occurred in (Table 2). Three-day old larvae were preferred to 5-day and



**Table 2.** Host age preference of *C. luteum* when offered equal numbers of different ages of FAW larvae under laboratory conditions

Host age combination (days)	Host instar	Mean $\pm$ SE (%)	P-value
3 vs 4	1st instar	43.33 $\pm$ 2.98a	0.646
	Early 2nd instar	44.67 $\pm$ 1.69a	
3 vs 5	1st instar	42.00 $\pm$ 2.49b	0.047
	Late 2nd instar	36.00 $\pm$ 1.94a	
3 vs 6	1st instar	44.67 $\pm$ 1.70a	<0.001
	3rd instar	25.33 $\pm$ 2.26b	
4 vs 5	Early 2nd instar	44.67 $\pm$ 1.33a	0.080
	Late 2nd instar	40.67 $\pm$ 2.21a	
4 vs 6	Early 2nd instar	40.67 $\pm$ 1.25b	<0.001
	3rd instar	23.33 $\pm$ 1.49a	
5 vs 6	Late 2nd instar	38.67 $\pm$ 1.70a	<0.001
	3rd instar	26.67 $\pm$ 1.50b	

Mean  $\pm$  standard error of different host instars of fall armyworm larvae parasitised when introduced simultaneously to *C. luteum*. Means followed by same letters within same columns are not significant different at  $P = 0.05$  probability level.

**Table 3.** Reproductive parameters and longevity of *Coccygidium luteum* reared on fall armyworm at  $28 \pm 1^\circ\text{C}$ 

Parameter	N	Mean $\pm$ SE	Range
Pre-oviposition period (days)	8	0.38 $\pm$ 0.51	0–1
Oviposition period (days)	8	5.13 $\pm$ 0.64	4–6
Post-oviposition period (days)	8	0	0
Lifetime parasitism	8	49.24 $\pm$ 24.0	31–66
Male longevity (days)	18	14.44 $\pm$ 1.43	11–17
Female longevity (days)	18	12.83 $\pm$ 1.12	10–15
Combined longevity (days)	36	13.64 $\pm$ 0.91	12–15
Female progeny/female	9	28.11 $\pm$ 8.18	9–47
Male progeny/female	9	39.89 $\pm$ 4.76	29–51

Mean duration of different reproductive parameters of *C. luteum*. N represents number of replications.

6-day old host larvae when both were presented simultaneously. Similarly, *C. luteum* parasitised higher numbers of 4-day old larvae than 6-day old larvae when they were presented together (Table 2). *C. luteum* attacked more 3-day old larvae followed by 4-day old larvae. Consistent with results from host-age susceptibility, host age preference for oviposition by *C. luteum* decreased with increasing larval age, demonstrating that *C. luteum* has preference for early instars of host larvae.

### Longevity and reproductive parameters of *C. luteum*

Female *C. luteum* began ovipositing a few hours after emergence. Pre-oviposition period varied from 0 to 24 hours and with a mean of  $0.38 \pm 0.51$  day (Table 3). Oviposition lasted for ca. 5 days (Table 3). No post-oviposition period was observed, as females continued to lay eggs until they died. Mean lifetime parasitism of the host larvae by *C. luteum* was  $49.24 \pm 24$  (Table 3). Adult *C. luteum* survived for ca. 14 days with no significant difference in

longevity of male and females ( $F = -0.887$ ;  $P = 0.381$ ) (Table 3). Progeny sex ratio was approximately 1.42 (Table 3). Generally, maternal age had no influence on number of female progenies except at 6-day old ( $t_{(12)} = 0.70$ ;  $P > 0.05$ ;  $P = 0.013$ ) (Fig. 1).

### Life cycle

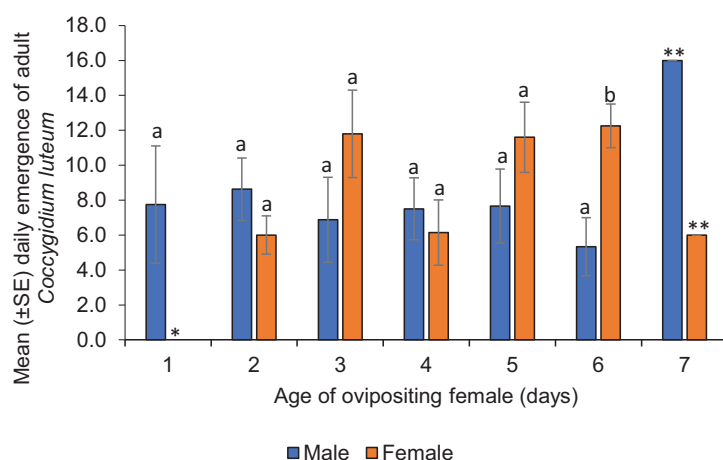
The mean developmental time of immature *C. luteum* from egg (oviposition) to cessation of feeding by the host was 8 days. The cessation of feeding to parasitoid grub (last instar of parasitoid larvae) egression from the host was 2 days. Thus, mean duration from oviposition to egression of final instar of the parasitoid larvae from the host cuticle was 10 days. From cocoon formation to adult parasitoids (wasp) egression lasted for 10 days (Table 4). Mean developmental period from oviposition to adult wasp emergence was 20 days (range 18–23) at a temperature of  $28 \pm 1^\circ\text{C}$  (Fig. 2).

### Discussion

The establishment of FAW in places outside of its origin is causing huge yield and economic losses to farmers (Abrahams *et al.*, 2017a; Kassie *et al.*, 2020; Overton *et al.*, 2021; Tambo *et al.*, 2023). This has necessitated the quest for sustainable management strategies that could be incorporated into integrated pest management. *Coccygidium luteum*, a koinobiont parasitoid, has been identified as a promising parasitoid that could help to reduce the damage caused by FAW (Agboyi *et al.*, 2019). In Ghana, it was among 10 parasitoid species identified as attacking FAW (Agboyi *et al.*, 2020). This study has revealed important information about *C. luteum* that could be utilised for the integrated management of FAW.

After oviposition by *C. luteum*, parasitised FAW larvae become less active than non-parasitised FAW. This is likely as a result of the injection of symbiotic polydnviruses or venoms from *C. luteum* which weakens the host (FAW) defences (Burke, 2016; Kacsoh and Schlenke, 2012; Wang *et al.*, 2021). More so, similar to the observation by Agboyi *et al.* (2019), parasitised larvae of FAW exhibited reduced growth rate and feeding compared to non-parasitised FAW. Parasitoid cocoon formation occurred within leaf tissues or beneath paper tissues placed in sauce cups. Exposed last instars of *C. luteum* larvae that emerged were dehydrated and died. In natural settings, the emergence of the final instars of *C. luteum* larvae from the host and subsequent cocoon formation likely occur in soil or plant debris.

In our study, *C. luteum* was able to parasitise and develop in three different larval instars (1st–3rd instars) of FAW. This indicates that *C. luteum* can parasitise different instars, specifically the early instar larvae of the host. This knowledge is crucial for establishing laboratory cultures of the parasitoid and mass rearing for biological control. It gives information on the susceptible host instar(s) of FAW for oviposition by *C. luteum*. Earlier studies, such as those on *C. gregarium*, suggested that *Coccygidium* spp. parasitise late instar larvae, which contrasts with our findings that *C. luteum* prefers early instar larvae (Sarmiento *et al.*, 2004). Our study provides new information that *C. luteum* prefers early instar larvae (i.e. 1st–3rd instars) of FAW. Both parasitism and preference tests in the present study demonstrated strong preference for early instar host larvae of FAW. Field collections of fourth to sixth instar FAW larvae yielded very few *C. luteum*, indicating low susceptibility of these late instar larvae to *C. luteum* attack. Furthermore, *C. luteum* was not able to parasitise late instar larvae of FAW when exposed to them in the laboratory. This may probably be because the host defence mechanisms might have been very active enabling



**Figure 1.** Influence of maternal age on the number of male and female progeny produced ( $n = 9$ ). Female progeny was significantly higher at day 6 ( $P = 0.013$ ). Parental males were made to mate with parental females in a separate 50 ml plastic vials for 24 hours prior to the females being exposed to FAW larvae. The asterisks \* and \*\* represent no adult female emergence and single count respectively so no analysis was done.

**Table 4.** Duration of developmental stages of *C. luteum* from oviposition to pupal stage ( $n = 9$ )

Parameter	No	Mean + SE	Range (days)
Oviposition to cessation of feeding by host	42	8.35 ± 0.06	7.50–9.50
Cessation of host feeding to parasitoid grub egression	42	1.91 ± 0.07	1.00–3.05
Oviposition to last instar of parasitoid egression	42	10.26 ± 0.07	9.00–11.28
Duration of cocoon formation	42	1.01 ± 0.00	0.94–1.11
Pupal period	42	9.08 ± 0.08	8.00–10.50

Number of days for various developmental stages of *C. luteum* within fall armyworm larvae as the host under laboratory conditions of  $28 \pm 1^\circ\text{C}$ ,  $70 \pm 5\%$  R.H., and L12:D12 photoperiod.

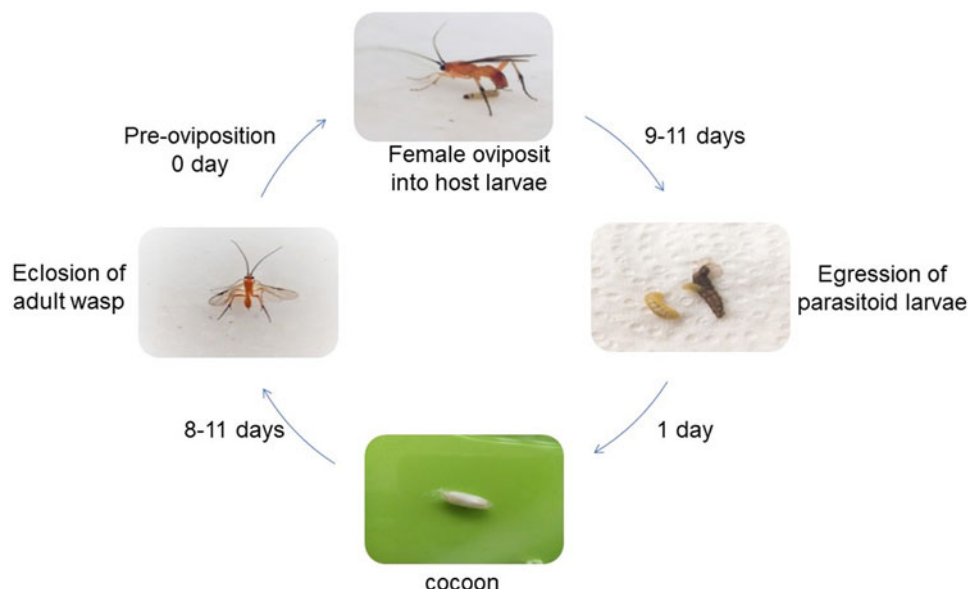
them to deter the parasitoids or encapsulate them (Vinson, 1980). Furthermore, the interaction between the age of a host and its acceptance for parasitism by parasitoids has been shown to vary between species (Queiroz *et al.*, 2019). It has also been shown that some parasitoid species are able to parasitise multiple host instars (Harvey *et al.*, 1994) while others prefer to parasitise single host instars (King, 1998; Mattiacci and Dicke, 1995). For example, the parasitoid *Tamarixia radiata* prefer late 4th–5th nymphal instars of the host *Diaphorina citri* (Sule *et al.*, 2014). In a related study, the larval parasitoid, *Cotesia marginiventris*, demonstrated preference for the 2nd instar of the host *S. litoralis* (Hegazi and Khafagi, 2024).

Our observation that *C. luteum* has preference for early instar larvae of FAW is good for biological control of FAW. This is because, preference for late instar larvae of FAW, would result in lots of damage to the maize plants by early instar FAW larvae before they are killed by the parasitoid in their late instar.

*Coccygidium luteum* was observed revisiting and ovipositing in previously parasitised hosts (superparasitism) under laboratory conditions. As a result, higher mortality was observed among 1st instar larvae after oviposition than other instars. This is supported by the fact that cannibalism among FAW larvae of same age is virtually absent in 1st and 2nd instars (Kasige *et al.*, 2022). In fact, the defence mechanisms of koinobiont parasitoids could be active and rely on the injection of venom proteins or a virus during oviposition, in order to compromise the immune system of the

host (Asgari *et al.*, 2003; Fang *et al.*, 2011; Yamanaka *et al.*, 1996). Multiple oviposition like the case of *C. luteum* may lead to overdose of venom, which could be lethal for the tiny first instar larvae of FAW. It is therefore presupposed that second instar larvae of FAW would be more suitable to be used in mass parasitism for biological control, as they were able to withstand superparasitism and exhibited very little to no cannibalism. The low parasitism of third instar FAW larvae by *C. luteum* may result from the larvae's ability to ward off the parasitoid or encapsulate it. Studies have shown that encapsulation increases with host age (Brodeur and Vet, 1995; Niogret *et al.*, 2009). The ability of *C. luteum* to parasitise early instars of the host larvae, coupled with the massive reduction in feeding by the parasitised larvae (Agboyi *et al.*, 2019) are desirable attributes making it a suitable candidate among larval parasitoids for augmentative biological control of FAW.

Lifetime parasitism rate of parasitoids is a major criterion for assessing their biological control potential. Parasitoids with high lifetime parasitism rates are advantageous in biological control as their parasitism rate facilitate rapid suppression of target hosts. The number of eggs a female FAW can lay in its lifetime is multiple folds higher than the number a female *C. luteum* can lay to parasitise larvae in its lifetime (Russianzi *et al.*, 2021). This notwithstanding, this study demonstrates that *C. luteum* can effectively parasitise a good number of host larvae. Observed lifetime parasitism may be influenced by the longevity of the parasitoid species (Souza *et al.*, 2014) as well as the parasitoid's ability to discriminate already parasitised hosts, thereby avoiding superparasitism and its associated egg wastage. Here, although the average longevity of virgin females of *C. luteum* was about 12 days, actual reproductive longevity under laboratory conditions was 7 days. This is in line with other studies on the negative effect of mating and oviposition on parasitoid longevity due to energy cost and resource allocation (Onagbola *et al.*, 2007). In the field, the crop environment and availability of preferred host instar among other factors could further influence the realised fecundity and effectiveness of *C. luteum*. It will be interesting to assess the potential fecundity of *C. luteum* which was not covered in this study. The variation in the mean development period of 20 days at  $28^\circ\text{C}$  to that observed by Agboyi *et al.* (2019) who reported a mean generation time of 16 days at  $32^\circ\text{C}$  was basically due to differences in the temperature at which the two experiments were conducted. Higher temperatures promote rapid developmental process and reduces developmental time hence the shorter developmental time observed at  $32^\circ\text{C}$  compared to  $28^\circ\text{C}$ .



**Figure 2.** Life cycle of *Coccygidium luteum* reared on fall armyworm under laboratory conditions of  $28 \pm 1^\circ\text{C}$ ,  $70 \pm 5\%$  R.H., and L12:D12 photoperiod.

Progeny sex ratio of parasitoids is influenced by several factors including maternal age. Indeed, several studies have demonstrated that sex ratio increase with maternal age (Santolamazza-Carbone *et al.*, 2007; Ueno, 2014). An earlier study has shown that the sex ratio in *Campoletis chloridae* was lower when the female was mated just after emergence and became male biased as maternal age increased (Pandey *et al.*, 2009). In this study, no influence of maternal age of *C. luteum* on progeny sex ratio was observed except on 6th day olds. The progeny sex ratio was highly variable and mainly male biased at the early stage. The highly male biased sex ratio at the early stage could be due to delay in fertilisation resulting in laying of unfertilised eggs and the fact that braconid parasitoids such as *C. luteum* exhibit haplodiploidy where unfertilised eggs develop into males.

In conclusion, this study provides vital information that can be utilised in exploring *C. luteum* for biological control. It also serves as a reference in future studies on other members of this untapped genus. Further studies are however needed to understand other biological parameters such as the determinants of sex ratio, release density, and frequency, that may influence the efficacy of *C. luteum* as a biological control agent.

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**Author contributions.** Patrick Beseh: conceptualisation, design, experimentation, and writing of manuscript. Benjamin Mensah: review, editing, and supervision. John Abraham: review, editing, and supervision. Lakpo Koku Agboyi: data analysis, review, editing, and supervision.

**Competing interests.** We hereby declare that there is no conflict of interest that could have arisen from the work presented in this paper.

## References

- Abang AF, Nanga SN, Kuate AF, Kouebou C, Suh C, Masso C, Saethre MG and Mokpokpo Fiaboe KK (2021) Natural enemies of fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in different agro-ecologies. *Insects* 12(6), 1–23. doi:10.3390/insects12060509
- Abbas A, Ullah F, Hafeez M, Han X, Dara MZN, Gul H and Zhao CR (2022) Biological control of fall armyworm, *Spodoptera frugiperda*. *Agronomy* 12(11), 2704. doi:10.3390/agronomy12112704
- Abraham J, Benhotons GS, Krampah I, Tagba J, Amissah C and Abraham JD (2018) Commercially formulated glyphosate can kill non-target pollinator bees under laboratory conditions. *Entomologia Experimentalis Et Applicata* 166(8), 695–702. doi:10.1111/eea.12694
- Abrahams P, Beale T, Cock M, Corniani N, Day R and Godwin J (2017a). Fall Armyworm Status: Impacts and Control Options in Africa: Preliminary evidence note. Cabi, April, 18 pp.
- Agboyi LK, Goergen G, Beseh P, Mensah SASA, Clottey VAVA, Glikpo R, Buddie A, Cafà G, Offord L, Day R, Rwomushana I and Kenis M (2020) Parasitoid complex of fall armyworm, *Spodoptera frugiperda*, in Ghana and Benin. *Insects* 11(2), 68. doi:10.3390/insects11020068
- Agboyi LK, Mensah SA, Clottey VA, Beseh P, Glikpo R, Rwomushana I, Day R and Kenis M (2019) Evidence of leaf consumption rate decrease in fall armyworm, *Spodoptera frugiperda*, larvae parasitized by *Coccygidium luteum*. *Insects* 10(11). doi:10.3390/insects10110410
- Ahissou BR, Sawadogo WM, Bokonon-Ganta AH, Somda I and Verheggen F (2021a) Integrated pest management options for the fall armyworm *Spodoptera frugiperda* in West Africa: Challenges and opportunities. A review. *Biotechnology, Agronomy and Society and Environment* 25(3), 192–207. doi:10.25518/1780-4507.19125
- Amalin DM, Peña JE and Duncan RE (2005) Effects of host age, female parasitoid age, and host plant on parasitism of *Ceratogramma etiennei* (Hymenoptera: Trichogrammatidae). *Florida Entomologist* 88(1), 77–82. doi:10.1653/0015-4040(2005)088[0077:EOHAFP]2.0.CO;2
- Asgari S, Zareie R, Zhang G and Schmidt O (2003) Isolation and characterization of a novel venom protein from an endoparasitoid, *Cotesia rubecula* (Hym: Braconidae). *Archives of Insect Biochemistry and Physiology* 53(2), 92–100. doi:10.1002/arch.10088



- Boaventura D, Martin M, Pozzebon A, Mota-Sanchez D and Nauen R** (2020) Monitoring of target-site mutations conferring insecticide resistance in *Spodoptera frugiperda*. *Insects* **11**(8), 1–15. doi:[10.3390/insects11080545](https://doi.org/10.3390/insects11080545)
- Brodeur J and Vet LEM** (1995) Relationships between parasitoid host range and host defence: A comparative study of egg encapsulation in two related parasitoid species. *Physiological Entomology* **20**(1), 7–12. doi:[10.1111/j.1365-3032.1995.tb00794.x](https://doi.org/10.1111/j.1365-3032.1995.tb00794.x)
- Burke GR** (2016) Analysis of genetic variation across the encapsidated genome of *Microplitis demolitor* bracovirus in parasitoid wasps. *PLoS One* **11**(7), 1–20. doi:[10.1371/journal.pone.0158846](https://doi.org/10.1371/journal.pone.0158846)
- Canico A, Mexia A and Santos L** (2020) First report of native parasitoids of fall armyworm *Spodoptera frugiperda* smith (Lepidoptera: Noctuidae) in Mozambique. *Insects* **11**(9), 1–12. doi:[10.3390/insects11090615](https://doi.org/10.3390/insects11090615)
- Capinera JL** (2020) Featured Creatures: Fall armyworm. [https://entnemdept.ufl.edu/creatures/field/fall\\_armyworm.htm](https://entnemdept.ufl.edu/creatures/field/fall_armyworm.htm) (accessed 07 December 2024).
- De Souza AR, Candelaria MC, Barbosa LR, Wilcken CF, Campos JM, Serrão JE and Zanuncio JC** (2016) Longevity of *Cleruchoides noackae* (Hymenoptera: Mymaridae), An Egg Parasitoid of *Thaumastocoris peregrinus* (Hemiptera: Thaumastocoridae), with Various Honey Concentrations and at Several Temperatures. *Florida Entomologist* **99**(1), 33–37. doi:[10.1653/024.099.0107](https://doi.org/10.1653/024.099.0107)
- Durocher-Granger L, Tibonge M, Musesha M, Lowry L, Reynolds K, Buddie A, Cafà G, Offord L, Chipabika G, Dicke M and Kenis M** (2021) Factors influencing the occurrence of fall armyworm parasitoids in Zambia. *J Pest Sci* **94**(4), 1133–1146. doi:[10.1007/s10340-020-01320-9](https://doi.org/10.1007/s10340-020-01320-9)
- Fang Q, Wang F, Gatehouse JA, Gatehouse R, M. A, Chen X, Hu C and Ye G** (2011) Venom of parasitoid, *Pteromalus puparum*, suppresses host, *Pieris rapae*, immune promotion by decreasing host C-type lectin gene expression. *PLoS One* **6**(10), 1–15. doi:[10.1371/journal.pone.0026888](https://doi.org/10.1371/journal.pone.0026888)
- Ghramh HA** (2011) Records of the genus *Coccygidium saussure* (Hymenoptera: Braconidae: Agathidinae), with description of a new species from Saudi Arabia. *African Journal of Biotechnology* **10**(42), 8481–8483. doi:[10.5897/ajb11.597](https://doi.org/10.5897/ajb11.597)
- Goergen G, Kumar PL, Sankung SB, Togola A and Tamò M** (2016) First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in West and Central Africa. *PLoS One* **11**(10), 1–9. doi:[10.1371/journal.pone.0165632](https://doi.org/10.1371/journal.pone.0165632)
- Harvey JA, Harvey IF and T DJ** (2014) Flexible larval growth allows use of a range of host sizes by a parasitoid wasp. *Ecological Society of America* **75**(5), 1420–1428.
- Harvey Jeffery A, Harvey IF, and Thompson DJ** (1994) Flexible larval growth allows use of a range of host sizes by parasitoid wasp. *Ecological Society of America* **75**(5), 1420–1428.
- Hegazi E and Khafagi W** (2024) Host-instar selection, interspecific competition, and reproductive capacity of extant and novel parasitoids (Hymenoptera: Braconidae) on Egyptian cotton leafworm. *Egyptian Journal of Biological Pest Control* **34**(1), 10. doi:[10.1186/s41938-024-00770-y](https://doi.org/10.1186/s41938-024-00770-y)
- Ihara M, Buckingham SD, Matsuda K, Sattelle DB, Ihara M, Buckingham SD and Matsuda K** (2017) Modes of action, resistance and toxicity of insecticides targeting nicotinic acetylcholine receptors. *Current Medicinal Chemistry* **24**(27), 2925–2934. doi:[10.2174/0929867324666170206142019](https://doi.org/10.2174/0929867324666170206142019)
- Kacsoh BZ and Schlenke TA** (2012) High hemocyte load is associated with increased resistance against parasitoids in *Drosophila suzukii*, a relative of *D. melanogaster*. *PLoS One* **7**(4). doi:[10.1371/JOURNAL.PONE.0034721](https://doi.org/10.1371/JOURNAL.PONE.0034721)
- Kansiime MK, Mugambi I, Rwomushana I, Nunda W, Lamontagne-Godwin J, Rware H, Phiri NA, Chipabika G, Ndlovu M and Day R** (2019). Farmer perception of fall armyworm (*Spodoptera frugiperda* J.E. Smith) and farm-level management practices in Zambia. [10.1002/ps.5504](https://doi.org/10.1002/ps.5504)
- Kasige RH, Dangalle CD, Pallewatta N and Perera MTMDR** (2022) Laboratory studies of larval cannibalism in same-age conspecifics of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera, Noctuidae) in maize. *Tropical Agricultural Research and Extension* **25**(1), 85. doi:[10.4038/TARE.V25I1.5559](https://doi.org/10.4038/TARE.V25I1.5559)
- Kassie M, Wossen T, De Groote H, Tefera T, Sevgan S and Balew S** (2020) Economic impacts of fall armyworm and its management strategies: Evidence from southern Ethiopia. *European Review of Agricultural Economics* **47**(4), 1473–1501. doi:[10.1093/erae/jbz048](https://doi.org/10.1093/erae/jbz048)
- King BH** (1998) Host age response in the parasitoid wasp *Spalangia cameroni* (Hymenoptera: Pteromalidae). *Journal of Insect Behavior* **11**(1), 103–117. doi:[10.1023/A:1020822717975](https://doi.org/10.1023/A:1020822717975)
- Kumar RM, Gadratagi BG, Paramesh V, Kumar P, Madivalar Y, Narayanappa N and Ullah F** (2022) Sustainable management of invasive fall armyworm, *Spodoptera frugiperda*. *Agronomy* **12**(9), 2150. doi:[10.3390/agronomy12092150](https://doi.org/10.3390/agronomy12092150)
- Mattiacci L and Dicke M** (1995) Host-age discrimination during host location by *Cotesia glomerata*, a larval parasitoid of *Pieris brassicae*. *Entomologia Experimentalis Et Applicata* **76**(1), 37–48. doi:[10.1111/j.1570-7458.1995.tb01944.x](https://doi.org/10.1111/j.1570-7458.1995.tb01944.x)
- Montezano DG, Specht A, Sosa-Gómez DR, Roque-Specht VF, Sousa-Silva JC, Paula-Moraes SV, Peterson JA and Hunt TE** (2018) Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. *African Entomology* **26**(2), 286–300. doi:[10.4001/003.026.0286](https://doi.org/10.4001/003.026.0286)
- Niogret J, Sait SM and Rohani P** (2009) Parasitism and constitutive defence costs to host life-history traits in a parasitoid-host interaction. *Ecological Entomology* **34**(6), 763–771. doi:[10.1111/j.1365-2311.2009.01131.x](https://doi.org/10.1111/j.1365-2311.2009.01131.x)
- Onagbola EO, Fadamiro HY and Mbata GN** (2007) Longevity, fecundity, and progeny sex ratio of *Pteromalus cerealellae* in relation to diet, host provision, and mating. *Biological Control* **40**(2), 222–229. doi:[10.1016/j.biocontrol.2006.10.010](https://doi.org/10.1016/j.biocontrol.2006.10.010)
- Otim MH, Aropet SA, Opio M, Kanyesigye D, Opolot HN and Tay WT** (2021) Parasitoid distribution and parasitism of the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in different maize producing regions of Uganda. *Insects* **12**(2), 1–20. doi:[10.3390/INSECTS12020121](https://doi.org/10.3390/INSECTS12020121)
- Overton K, Maino JL, Day R, Umina PA, Bett B, Carnovale D, Ekesi S, Meagher R and Reynolds OL** (2021) Global crop impacts, yield losses and action thresholds for fall armyworm (*Spodoptera frugiperda*): A review. *Crop Protection* **145**(March), 105641. doi:[10.1016/j.cropro.2021.105641](https://doi.org/10.1016/j.cropro.2021.105641)
- Pandey AK, Tripathi S and Tripathi CPM** (2009) Effects of parental age at mating on the fecundity and progeny sex ratio of *Campoplex chloridiae*, an endolaryval parasitoid of the pod borer, *Helicoverpa armigera*. *BioControl* **54**(1), 47–53. doi:[10.1007/s10526-007-9149-2](https://doi.org/10.1007/s10526-007-9149-2)
- Qi GJ, Ma J, Wan J, Ren YL, McKirdy S, Hu G and Zhang ZF** (2021) Source regions of the first immigration of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) invading Australia. *Insects* **12**(12). doi:[10.3390/insects12121104](https://doi.org/10.3390/insects12121104)
- Queiroz AP, Favetti BM, Hayashida R, Grande MLM, Neiva MM, Panizzi AR and Bueno AF** (2019) Effect of the ages of parasitoid and host eggs on *Telenomus podisi* (Hymenoptera: Platygastridae) parasitism. *Neotropical Entomology* **48**(6), 974–982. doi:[10.1007/s13744-019-00724-2](https://doi.org/10.1007/s13744-019-00724-2)
- Russianzi W, Anwar R and Triwidodo H** (2021) Biostatistics of fall armyworm *Spodoptera frugiperda* in maize plants in Bogor, West Java, Indonesia. *Biodiversitas* **22**(6), 3463–3469. doi:[10.13057/biodiv/d220655](https://doi.org/10.13057/biodiv/d220655)
- Santolamazza-Carbone S, Nieto MP and Rivera AC** (2007) Maternal size and age affect offspring sex ratio in the solitary egg parasitoid *Anaphes nitens*. *Entomologia Experimentalis Et Applicata* **125**(1), 23–32. doi:[10.1111/j.1570-7458.2007.00595.x](https://doi.org/10.1111/j.1570-7458.2007.00595.x)
- Sarmiento CE, Sharkey MJ and Janzen DH** (2004) The first gregarious species of the Agathidinae (Hymenoptera: Braconidae). *Journal of Hymenoptera Research* **13**(2), 295–301.
- Sharkey MJ and Chapman EG** (2017) Phylogeny of the Agathidinae (Hymenoptera: Braconidae) with a revised tribal classification and the description of a new genus. *Proceedings of the Entomological Society of Washington* **119**, 823–842. doi:[10.4289/0013-8797.119.SpecialIssue.823](https://doi.org/10.4289/0013-8797.119.SpecialIssue.823)
- Shiferaw B, Prasanna BM, Hellin J and Bänziger M** (2011) Crops that feed the world 6. Past successes and future challenges to the role played by maize in global food security. *Food Security* **3**, 307–327. doi:[10.1007/s12571-011-0140-5](https://doi.org/10.1007/s12571-011-0140-5)
- Sisay B, Simiyu J, Malusi P, Likhayo P, Mendesil E, Elibariki N, Wakgari M, Ayalew G and Tefera T** (2018) First report of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), natural enemies from Africa. *Journal of Applied Entomology* **142**(8), 800–804. doi:[10.1111/jen.12534](https://doi.org/10.1111/jen.12534)

- Srikanth J, Geetha N, Singaravelu B, Ramasubramanian T, Mahesh P, Saravanan L, Salin KP, Chitra N and Muthukumar M (2018) First report of occurrence of fall armyworm *Spodoptera frugiperda* in sugarcane from Tamil Nadu, India. *Pest Management in Horticultural Ecosystems* **24**(1), 23–28.
- Sule H, Muhamad R, Omar D and Kah-Wei Hee A (2014) Parasitism rate, host stage preference and functional response of *Tamarixia radiata* on *Diaphorina citri*. *International Journal of Agriculture and Biology* **16**(4), 783–788. [https://www.researchgate.net/publication/286292067\\_Parasitism\\_Rate\\_Host\\_Stage\\_Preference\\_and\\_Functional\\_Response\\_of\\_Tamarixia\\_radiata\\_on\\_Diaphorinacitri/citation/download](https://www.researchgate.net/publication/286292067_Parasitism_Rate_Host_Stage_Preference_and_Functional_Response_of_Tamarixia_radiata_on_Diaphorinacitri/citation/download)
- Tabebordbar F, Shishehbor P, Ebrahimi E, Polaszek A and Riddick EW (2022) Parasitoid age and host age interact to improve life history parameters and rearing of *Trichogramma euproctidis*. *Biocontrol Science and Technology* **32**(3), 267–280. doi:10.1080/09583157.2021.1990858
- Tambo JA, Day RK, Lamontagne-Godwin J, Silvestri S, Beseh PK, Oppong-Mensah B, Phiri NA and Matimelo M (2020) Tackling fall armyworm (*Spodoptera frugiperda*) outbreak in Africa: An analysis of farmers' control actions. *International Journal of Pest Management* **66**(4). doi:10.1080/09670874.2019.1646942
- Tambo JA, Kansime MK, Mugambi I, Agboyi LK, Beseh PK and Day R (2023) Economic impacts and management of fall armyworm (*Spodoptera frugiperda*) in smallholder agriculture: A panel data analysis for Ghana. *CABI Agriculture and Bioscience* **4**(1), 1–14. doi:10.1186/s43170-023-00181-3
- Ueno T (2014) Age-dependent constraints of sex allocation in a parasitoid wasp. *Psyche (London)* **2014**, 1–4. doi:10.1155/2014/363174
- Ullah S and Shad SA (2017) Toxicity of insecticides, cross-resistance and stability of chlorfenapyr resistance in different strains of *Oxycarenus hyalinipennis* Costa (Hemiptera: Lygaeidae). *Crop Protection* **99**, 132–136. doi:10.1016/j.cropro.2017.05.019
- Vinson SB and Iwantsch GF (1980) Host suitability for insect parasitoids. *Annual Review Entomology* **44**(25), 397–419. doi:0066-4170/80/0101-0397
- Wang Z, Ye X, Zhou ID Y, Wu ID X, Hu R, Zhu J, Chen T, Huguet ID E, Shi ID M, Drezen J-M, Huang ID J and Chen ID X (2021) Bracoviruses recruit host integrases for their integration into caterpillar's genome. doi:10.1371/journal.pgen.1009751
- Yamanaka A, Hayakawa Y, Noda H, Nakashima N and Watanabe H (1996) Characterization of polydnavirus-encoded mRNA in parasitized armyworm larvae. *Insect Biochemistry and Molecular Biology* **26**(6), 529–536. doi:10.1016/0965-1748(95)00107-7