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The parasitoid *Trichogrammatoidea armigera* Nagaraja (Hymenoptera: Trichogrammatidae) is a potential candidate for biological control of the millet head miner *Heliocheilus albipunctella* (de Joannis) (Lepidoptera: Noctuidae) in the Sahel

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1. Introduction

Pearl millet, *Pennisetum glaucum* (L.) R. Br., is a crop grown throughout West Africa, especially in the Sahel. Pearl millet is the major staple food for the population of the Sahel, particularly for household use. It is one of the world's most resilient drought-tolerant cereal crops, surviving even in the poorest soils in the driest regions and in the hottest climates. Despite this extreme climatic adaptation, pearl millet suffers from many biotic constraints, including insect pests (Nwanze and Harris, 1992). Among these, the stem borer (MSB) *Coniesta ignefusalis* (Hampson) (Lepidoptera: Crambidae) and the millet head miner (MHM) *Heliocheilus albipunctella* (de Joannis) (Lepidoptera: Noctuidae) are the major chronic insect pests of millet in the Sahel, including Niger. The MSB develops on many species of the Poaceae family; in the Sahel, it develops 2–3 generations per year on pearl millet during the rainy season and diapauses in leftover pearl millet stems during the rest of the year (Youm et al., 1996). The damage from *C. ignefusalis* is due to the feeding of developing larvae in millet stalks; first generation larvae cause dead hearts and stand loss, while the second and third generations cause lodging, disruption of the vascular system, and inhibition of grain formation (Harris, 1962; Youm et al., 1996). The MHM is a univoltine and monophagous species, which develops on millet in the Sahel during the rainy season between July and October and spends the remainder of the season in diapause in the soil (Gahukar et al., 1986). Infestations of *H. albipunctella* are more severe in the drier zones of the Sahel (Nwanze and Harris, 1992). The damage from *H. albipunctella* is due to larvae that feed on the panicle and prevent grain formation (Nwanze and Harris, 1992). Almost every year, outbreaks of the MHM are observed in the Sahel, especially on millet planted early or early-maturing cultivars, while millet planted later or late-maturing cultivars is more affected by MSB (Gahukar et al., 1986; Youm et al., 1996). Both insect pests inflict significant yield losses ranging from 15% to total crop failure for *C. ignefusalis* (Harris, 1962; Ajayi, 1990) and from 40% to 85% for *H. albipunctella* (Gahukar et al., 1986; Krall et al., 1995).

Control strategies for these two insect pests, including cultural management, host plant resistance and the use of insecticides (Gahukar et al., 1986; Youm et al., 1996), have been tested with limited success and applicability (Nwanze and Harris, 1992; Ndoye and Gahukar, 1995).

Augmentative biological control was recently successfully tested in the Sahel for controlling the MHM with releases of the parasitoid wasp *Habrobracon hebetor* Say (Hymenoptera: Braconidae) with up 90% mortality of MHM (Payne et al., 2011; Ba et al., 2013, 2014; Baoua et al., 2014). So far, the biological control of the MHM with the parasitoid *H. hebetor* only targeted the third and later instar larvae of the MHM when the insect had already started feeding on millet grains. Early control of MHM might be better achieved with releases of egg parasitoids, especially *Trichogramma* species, as they are usually inexpensive and easy to produce in large numbers (Wang et al., 2014).

Surveys on MHM egg parasitoids in the Sahel reported the presence of an unidentified *Trichogrammatoidea* species (Bal, 1993; Garba and Gaoh, 2008), which was later identified as *Trichogrammatoidea armigera* Nagaraja (Hymenoptera: Trichogrammatidae) (Sow et al., 2018). The natural enemies of the MSB include a larval parasitoid, *Syzeuctus* sp. (Hymenoptera: Ichneumonidae), and an egg parasitoid, *Telenomus busseolae* Gahan (Hymenoptera: Scelionidae) (Youm et al., 1996). Because of the challenges of mass culturing these parasitoids, augmentative biological control of the MSB has never been attempted in the region.

The overall objective of this study was to evaluate the natural parasitism by *T. armigera* on the MHM and to assess it effectiveness for controlling the MHM. In addition, the study aimed to identify alternate hosts among available lepidopteran species of pearl millet and other cultivated crops that could sustain *T. armigera* population. Finally, we

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assessed the suitability of factitious hosts among available storage lepidopteran species for mass culturing the trichogrammatid parasitoid for use in augmentative releases.

2. Materials and methods

2.1. Study environment

Scouting for egg parasitoids was carried out in Niger from 2014 to 2016 in an area that lies between latitudes 13°01′ and 14°09′N, and longitudes 0°43′ and 4°01′E. The research sites belong to the Sahel agroecological zone, which has a unimodal rainfall pattern, and the rainy season lasts from June to October. Pearl millet is the main cereal crop, covering almost 95% of the cropping area, usually in association with cowpea. Pearl millet is cultivated between June and October under rainfed conditions. A total annual rainfall of 752 mm, 534 mm, and 411 mm was recorded in 2014, 2015, and 2016, respectively.

The eggs of the MHM were encountered from August to mid-September under a temperature of 27.8 ± 3.5 °C and a relative humidity of 76.2 ± 15.7%.

The lab bioassays were carried out in the entomology laboratory of ICRISAT at Sadore under a temperature of 27.8 ± 1 °C and a relative humidity of 85.46 ± 0.5%.

2.2. Insect cultures for bioassays

For the purpose of these experiments, we used readily available lepidopteran insect pests occurring on crops and storage commodities in Niger that could be used for *T. armigera* mass rearing and/or alternate hosts for survival during the off-season when MHM is in diapause.

In addition to the millet head miner, *Heliocheilus albipunctella* (de Joannis) (Lepidoptera: Noctuidae), the field insect pests included the millet stem borer, *Coniesta ignefusalis* (Hampson) (Lepidoptera: Crambidae), the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) and the moringa tree (*Moringa oleifera* Lam.) leaf defoliator, *Noorda blitealis* (Walker) (Lepidoptera: Crambidae). The MSB was added because it belongs to the same MHM ecosystem and could share some natural enemies. *H. armigera* and *N. blitealis* were included as potential alternate hosts present, respectively, on tomato during the off-season and all year round on the moringa tree. The moths of *H. albipunctella*, *C. ignefusalis* and *H. armigera* were collected from 5 light traps that were set up on the 500 ha area of the ICRISAT Sadore campus (latitude 13°15′N, longitude 2°18′E). The light trap utilized a 250-W mercury vapor white incandescent bulb wired to the grid. The bulb was positioned above a wire mesh cage (1.38 with × 1.93 m height), which rested on a metal support set 2.43 m above the ground level. The light trap was operated from June to October 2016 and caught moths of the aforementioned species were taken to egg-laying wire mesh cages (30 cm × 30 cm) in the laboratory. A sheet of paper was placed at the bottom of the cages, and eggs were collected daily and used for the different bioassays. Different species were placed in different laying cages, and wool or cotton soaked with sugar (10% sucrose in water solution) was hung in the cages to feed the moths. In the case of *H. albipunctella*, the moths were supplied every morning with newly emerging millet panicles (collected from the millet field set for the purpose) on which to lay eggs overnight. Moths of the moringa leaf defoliant *N. blitealis* were collected from a culture established in the laboratory from caterpillars collected on moringa trees at the ICRISAT Campus in Sadore. The larvae were reared in small cylindrical plastic vials (ø = 4.5 cm; h = 11.5 cm) and given fresh moringa leaves as a feeding substrate. The larvae completed development within 15 days. Emerging moths were taken to laying cages and eggs were collected on a sheet of paper placed at the bottom of the cages. Typically, moths laid eggs for 4 days.

The storage lepidopteran species included the rice moth, *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae), the Mediterranean floor moth, *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae), and the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae). The storage species were chosen as potential factitious hosts for mass culturing *T. armigera*. A colony of each of the three insects was established in the laboratory at ICRISAT Sadore from wild insects collected in farmers' granaries in Niger in 2015. The insects are routinely reared on a mixture of pearl millet grain and flour in plastic buckets at ambient temperature. Usually, adults emerged after one month.

2.3. Evaluating the natural parasitism of the MHM and the MSB

Eggs of the MHM were collected every rainy season (August-September) from 2014 to 2016 in farmers' pearl millet fields in different environments of Niger (9 villages in 2014, 7 villages in 2015 and 17 villages in 2016) in approximately 100 farms every year. The eggs are usually found at the top of panicles (Gahukar et al., 1986). The eggs were collected from approximately 5000 panicles every year and were reared in the laboratory at ambient temperature until the emergence of parasitoids. The natural parasitism was assessed based on the number of parasitized eggs out of the total number of collected eggs (5700–7000 eggs). Emerging parasitoids were identified and sexed. While collecting eggs of the MHM, the development stage of the pearl millet head (newly emerged heads, flowering heads, heads with milk grains) was also recorded. Similarly, the cycle of the variety (early maturing, late maturing) on which the eggs were collected was also recorded. The earliness or lateness of a plant in this case could be either attributed to the cultivar or the time of planting. Because eggs of the MSB are not easy to detect in the field, 800 irradiated sentinel eggs of MSB were glued every year on a square of cardboard (40 eggs/cardboard square/field) and placed on 20 randomly selected fields in pearl millet leaf-sheaths for parasitism for 6 days. Irradiation of eggs was performed in a dark chamber under UV light 4 W tube (UVP, USA, 254 nm) for 45mn at a distance of 3 cm.

2.4. Determining the demographic parameters of T. armigera

The *T. armigera* parasitoid population was initially started from field-collected eggs of the MHM from different regions of Niger. Eggs were kept in Petri dishes in the laboratory at the ambient conditions described above until emergence of the adults. Emerging *T. armigera* were collected daily and placed in tubes containing freshly laid eggs of the rice moth, *C. cephalonica*. The host eggs (N = 125) were glued on white rectangular cards (7.5 cm × 2.5 cm), and a drop of honey was placed at the corner of the card as food for adult parasitoids. We initially confined variable numbers (N = 1–30) of mated females of the parasitoid with 125 eggs of *C. cephalonica* for parasitism. Once the population of *T. armigera* was successfully established, we determined the demographic parameters of the parasitoid. To investigate life-long fecundity, 10 mated females of *T. armigera* were daily supplied individually with 30 fresh eggs of *C. cephalonica* for parasitism until death. From each female, we recorded the number of parasitized eggs, parasitized eggs with viable progeny, egg to adult development time, number of progeny and the sex ratio of emerging adults.

2.5. Acceptability of different Lepidoptera species to T. armigera

This experiment was conducted in two phases. First, under no-choice conditions, eggs of seven different lepidopteran species (*C. ignefusalis, C. cephalonica*, *E. kuehniella, H. albipunctella*, *H. armigera*, *N. blitealis* and *S. cerealella*) were exposed to newly emerging *T. armigera* mated females. Eggs (N = 125) of each species were glued on a card (7.5 cm × 2.5 cm) and placed in a vial, together with 5 mated *T. armigera* females for 48 h. A total of 32 cards/species, representing 32

replicates, were prepared. The vials were incubated until the emergence of the new generation of *T. armigera* adults. Data on parasitism, emerging adult and development time from eggs to adults were recorded.

This first experiment was followed by another set of experiments under no-choice and multiple-choice conditions with 4 different species (*C. ignefusalis, C. cephalonica, H. armigera and H. albipunctella*). Under no-choice conditions, the eggs of the 4 different species were kept separate in different vials and infested with one mated *T. armigera* female. For each species, 30 eggs were glued on a separate card, placed in a vial and confined with one mated *T. armigera* female for 48 h. A total of 24 cards/species, representing 24 replicates, were prepared. Data on parasitism was recorded. Under the multiple-choice condition, 30 eggs of each of the 4 different species (*C. ignefusalis, C. cephalonica, H. armigera and H. albipunctella*) were all glued on a single card (7.5 cm × 2.5 cm) and given to newly emerged *T. armigera* mated females to parasitize. Eggs of the 4 species were not mixed together; eggs of each species were glued on one corner of the card. The cards were put individually in a vial and confined with one mated *T. armigera* female for 48 h. A total of 20 cards in 20 vials representing 20 replicates were prepared. The vials were incubated until the emergence of the new generation of *T. armigera* adults. Data on parasitism was recorded.

2.6. Assessment of the suitable egg density for parasitism by T. armigera

The experiments consisted of determining the egg density needed for *T. armigera* parasitism. The test was carried out with 3 different host species (*C. ignefusalis, C. cephalonica,* and *H. albipunctella*). For each host species, the treatments were as follows: i) one (1) *T. armigera* female confined with 10 eggs of one host species; ii) one (1) *T. armigera* female confined with 30 eggs of one host species; and iii) one (1) *T. armigera* female confined with 125 eggs of one host species. For each treatment and each host species, we used 12 replicates. The female parasitoid and eggs were confined for 6 days, corresponding to the period in which new progeny will start emerging. Data on parasitism and emerging adults was collected.

2.7. Assessment of intraspecific competition by T. armigera

In this experiment a set of 125 eggs of 3 different host species (*C. ignefusalis, C. cephalonica,* and *H. albipunctella*) were given to increasing numbers of *T. armigera* females for parasitism. For each host species, the treatments were as follows: i) one (1) *T. armigera* female confined with 125 eggs of one host species; ii) five (5) *T. armigera* females confined with 125 eggs of one host species; iii) ten (10) *T. armigera* females confined with 125 eggs of one host species; and iv) thirty (30) *T. armigera* females confined with 125 eggs of one host species. For each treatment and each host species, we used 12 replicates. The female parasitoid and eggs were confined for 6 days, corresponding to the period in which new progeny will start emerging. Data on parasitism and emerging adults were collected.

2.8. Data analysis

Data were all subjected to an analysis of variance (ANOVA) (PROC GLM) with SAS software version 9.1 (SAS, 2003). When the ANOVAs were significant, means were compared by the Student-Newman-Keuls test at the 5% level.

3. Results

3.1. Natural parasitism of MHM and MSB eggs

The natural parasitism of MHM eggs ranged from 13% to 17%, with an average of 15.41 ± 1.79%. Newly emerging heads of early-maturing pearl millet bore more MHM eggs than the flowering and milk head stages (Table 1). The emerging heads of early-maturing pearl millet had significantly more parasitized eggs. Overall, newly emerged heads, regardless of maturing date, had significantly more eggs and more parasitized eggs (Table 1).

We did not encounter any parasitoids from sentinel MSB eggs.

3.2. Demographic parameters of T. armigera reared on eggs of C. cephalonica

The male of *T. armigera* had on average 2.32 ± 0.32 days life expectancy, which was extended to 3.38 ± 0.46 days when fed with honey. In the absence of the host species, *T. armigera* females had a lifespan of only 2.56 ± 0.33 days, which was extended to 4.03 ± 0.11 days when supplied with honey. When continually provided with host eggs, the *T. armigera* female lifespan was extended to 11.84 ± 0.06 days. The females parasitized 13.04 ± 0.62 eggs of *C. cephalonica* per day. On average 74.06 ± 3.46% of parasitized eggs of *C. cephalonica* yielded viable *T. armigera* progeny. On average, each *T. armigera* female had a total progeny average of 106.66 ± 16.87 individuals. The development from eggs to adults took on average 7.05 ± 0.03 days. *T. armigera* progeny started emerging 7 days after parasitization of *C. cephalonica* eggs and extended up to 20 days (Fig. 1). From day 7 to day 13, both sexes were represented, but afterwards, only males developed from parasitized eggs (Fig. 1). The sex ratio of the emerging *T. armigera* progeny was male-biased, with 2.17 times more males than females.

3.3. Host acceptability of T. armigera on different Lepidoptera species

Under no-choice conditions, when *T. armigera* was given eggs of different lepidopteran species, they significantly parasitized more eggs of *H. albipunctella* than the 5 other species (Table 2). However, significantly more parasitized eggs of *C. cephalonica* yielded viable offspring (Table 2). Significantly more offspring of *T. armigera* emerged from eggs of *C. cephalonica, H. albipunctella* and *E. kuehniella* compared to other species (Table 2). The duration of *T. armigera* egg to adult development was similar, regardless of host species (Table 2).

When given eggs of *H. albipunctella, C. cephalonica, C. ignefusalis* and *H. armigera, T. armigera*, females parasitized significantly more eggs of *C. cephalonica* than the three other host species in both choice ($F_{3, 81} = 26.52$; $P < 0.001$) and no-choice situations ($F_{3, 92} = 198.67$, $P < 0.001$) (Fig. 2).

3.4. Optimum host/egg density for T. armigera parasitism and progeny development

The host/egg density significantly influenced the level of parasitism by *T. armigera* on all tested species, *H. albipunctella* ($F_{2\text{-}33} = 12.89$; $P < 0.001$), *C. cephalonica* ($F_{2\text{-}33} = 4.18$; $P = 0.02$) and *C. ignefusalis* ($F_{2\text{-}33} = 26.70$; $P < 0.001$) (Fig. 3). For all tested species, more offspring of *T. armigera* emerged when higher numbers of eggs were provided for parasitism (Table 3). The offspring/host eggs ratio varied between 0.23 and 0.60 for *H. albipunctella*, 0.46–0.52 for *C. cephalonica* and 0.04–0.11 for *C. ignefusalis*, the highest for each species being usually 1 *T. armigera* female for 30 eggs.

3.5. Parasitism level as a function of number of introduced parasitoids on different host species

In the presence of 125 eggs of the host species, the introduction of 1–30 females of *T. armigera* did not significantly affect the parasitism level on *H. albipunctella* ($F_{3\text{-}44} = 2.14$; $P = 0.10$), *C. cephalonica* ($F_{3\text{-}44} = 1.57$; $P = 0.20$) or *C. ignefusalis* ($F_{3\text{-}44} = 1.96$; $P = 0.13$) (Fig. 4). However, the number of emerging progeny did vary significantly for all tested host species, except for *C. ignefusalis* (Table 4). The number of emerging progeny/introduced parental *T. armigera* female ratio varied between 2.44 and 81.5 for *H. albipunctella*, 1.99 and 46.33 for *C.*

Table 1
Heads of millet bearing eggs of the MHM (% ± S.E) and natural parasitism of eggs due to *T. armigera* (% ± S.E) in Niger from 2014 to 2015 at different millet development stages and maturing dates. Within a column, means bearing different letters were significantly different (Student–Newman–Keuls test, α = 0.05).

Millet Head development stage	Type of millet	% Heads bearing MHM eggs (Means ± S.E.)	% Parasitized eggs (Means ± S.E.)
Newly emerged	Early-maturing	28.22 ± 2.48 a	12.56 ± 2.10 a
	Late-maturing	3.27 ± 1.33b	0.61 ± 0.43b
Flowering	Early-maturing	1.64 ± 0.71b	0.33 ± 0.18b
	Late-maturing	0.17 ± 0.17b	0.06 ± 0.06b
Milk stage	Early-maturing	2.08 ± 1.45b	0.00*
	Late-maturing	0.00*	0.00*
		$F_{5\text{-}240} = 53.97$; $P < 0.001$	$F_{5\text{-}245} = 19.67$; $P < 0.001$
Newly emerged		20.08 ± 2.10 a	8.66 ± 1.53 a
Flowering		1.13 ± 0.48b	0.24 ± 0.12b
Milk stage		1.09 ± 0.77b	0.00*
		$F_{2\text{-}243} = 58.67$; $P < 0.001$	$F_{5\text{-}248} = 25.21$; $P < 0.001$

* Not included in the ANOVA.

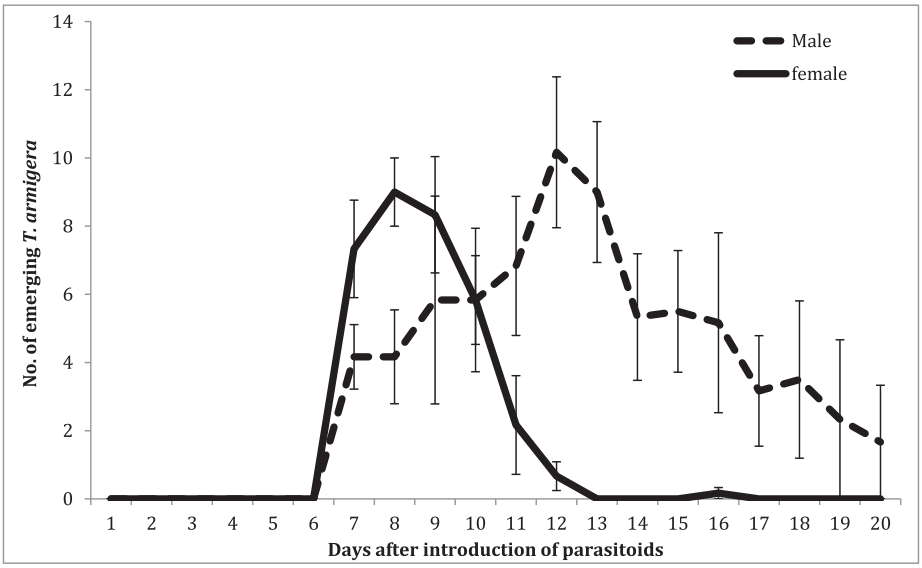

Fig. 1. Number (± S.E) of daily emerging *T. armigera* male and female progeny from parasitized *C. cephalonica* eggs.

cephalonica and 0.35 and 4.83 for *C. ignefusalis*, the highest for all species being 1 female *T. armigera* for 125 eggs.

4. Discussion

An endogenous parasitoid can only be used in biological control when highly effective against the target host. The parasitoids can either naturally control the pest without human intervention, or be protected or stimulated by habitat management, or subjected to augmentative releases (van Lenteren et al., 2018). In the case of millet, the larval parasitoid, *H. hebetor* is already being used with success for controlling the MHM (Kabore et al., 2017; Baoua et al., 2018). The addition of another parasitoid, especially a species targeting another developmental stage, such as eggs, would be complementary and could offer a better control of the pest. In this study, we identified the parasitoid, *T. armigera*, naturally parasitizing eggs of the MHM in the fields at levels as high as 17%. This is comparable to recent observation in Senegal (Sow et al., 2018), but higher than the 10% parasitism due to

Table 2
Parasitism of eggs of different host species due to *T. armigera*, parasitized eggs with progeny, total number of emerging progenies and development time (no choice conditions – N = 125 eggs of host for N = 5 *T. armigera* females). Within a column, means bearing different letters were significantly different (Student–Newman–Keuls test, α = 0.05).

Species	% Parasitized eggs (Mean ± S.E.)	% Parasitized eggs with offspring (Mean ± S.E.)	Total number of emerging parasitoids (Mean ± S.E.)	Development from eggs to adult (days ± S.E.)
H. albipunctella	79.86 ± 1.51 a	74.48 ± 1.65 abc	68.68 ± 2.77 a	7.07 ± 0.09 a
C. cephalonica	65.44 ± 2.57b	80.00 ± 2.10 ab	70.43 ± 5.48 a	7.06 ± 0.08 a
C. ignefusalis	28.79 ± 3.85 e	19.38 ± 4.41 d	6.18 ± 1.06 d	7.25 ± 0.08 a
H. armigera	57.57 ± 4.13 bc	63.41 ± 2.20 bc	44.93 ± 2.01b	7.00 ± 0.00 a
E. kuehniella	53.48 ± 3.94c	85.93 ± 10.79 a	58.93 ± 5.61 a	7.06 ± 0.13 a
S. cerealella	42.69 ± 3.78 d	59.95 ± 5.07c	30.81 ± 4.92c	7.34 ± 0.13 a
N. blitealis	30.27 ± 0.04 e	25.09 ± 0.16 d	9.65 ± 0.08 d	7.00 ± 0.00 a
	$F_{6\text{-}217} = 34.32$; $P < 0.0001$	$F_{6\text{-}217} = 27.80$; $P < 0.0001$	$F_{6\text{-}217} = 50.43$; $P < 0.0001$	$F_{6\text{-}217} = 2.01$; $P = 0.06$

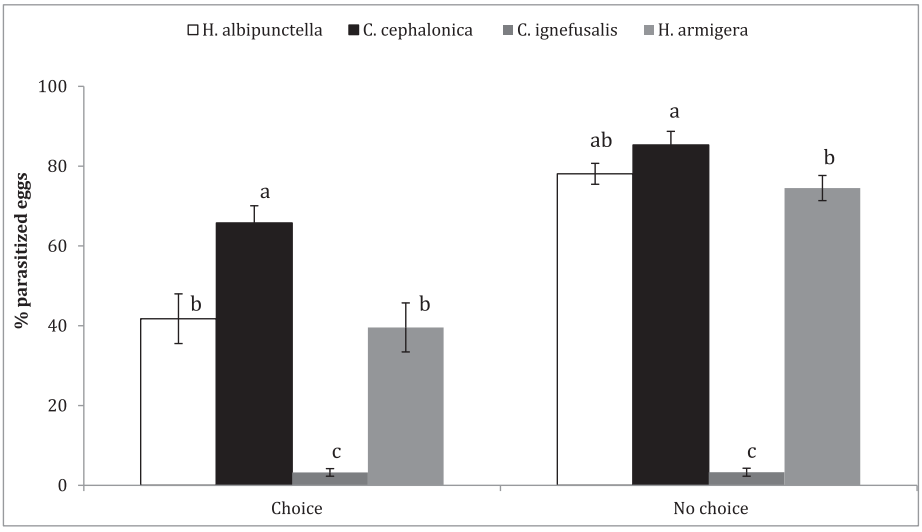

Fig. 2. Parasitism (% ± S.E) of eggs of *H. albipunctella*, *C. cephalonica*, *C. ignefusalis* and *H. armigera* by *T. armigera* in choice and no-choice conditions. For each choice or no choice test, column bearing different letters were significantly different (Student–Newman–Keuls test, α = 0.05).

Trichogrammatoidea spp. reported in Niger in 2004 (Garba and Gaoh, 2008). The same parasitoid was found parasitizing 60% of eggs of the MHM in Senegal in the late 1980s (Bal, 1993). The differences in the level of parasitism may be due to annual and location variability of the parasitoid importance and/or MHM relative abundance. In fact, the relative abundance of MHM could be influenced by pearl millet planting dates and flowering periods (Youm and Gilstrap, 1993; Sastawa et al., 2002), the varieties planted by farmers (Gahukar, 1990), and rainfall patterns (Nwanze and Sivakumar, 1990). Our data indicate higher numbers of eggs on the newly emerged heads, confirming the preference of this stage for oviposition by MHM as reported by Owusu et al. (2004). Moreover, this stage bore the highest parasitism by *T. armigera* as also observed by Bal (1993). This suggests a typical density dependent behavior as reported for related *Trichogrammatoidea* sp. nr. *lutea* (Girault) species (Kalyebi et al., 2005). Therefore, augmentative releases of *T. armigera* must be timely to coincide with highest densities

Table 3
Total number of *T. armigera* progeny emerging from different density eggs of *H. albipunctella*, *C. cephalonica* and *C. ignefusalis* parasitized with one *T. armigera* female (no choice condition). Within a column, means bearing different letters were significantly different (Student–Newman–Keuls test, α = 0.05).

Host egg density	No. emerging progeny of *T. armigera* (± S.E)		
	H. albipunctella	*C. cephalonica*	*C. ignefusalis*
10 eggs	7.00 ± 0.49c	4.83 ± 0.42c	0.66 ± 0.25c
30 eggs	17.33 ± 0.75b	15.66 ± 1.35b	3.33 ± 0.14b
125 eggs	75.50 ± 2.58 a	57.00 ± 6.05 a	5.66 ± 0.51 a
	$F_{2\text{-}33}$ = 54.62;	$F_{2\text{-}33}$ = 58.8;	$F_{2\text{-}33}$ = 53.88;
	P < 0.001	P < 0.001	P < 0.001

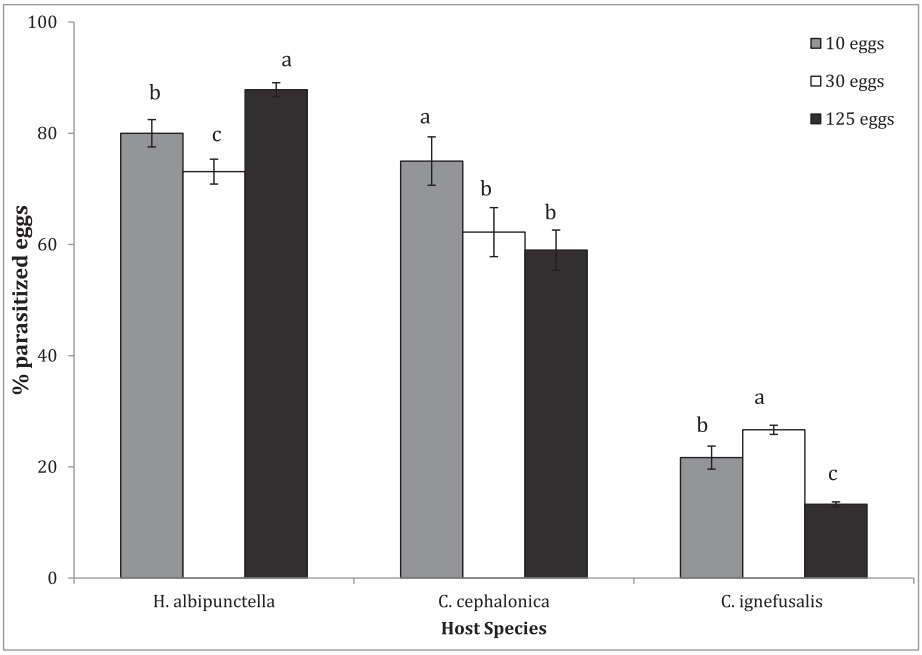

Fig. 3. Parasitism (% ± S.E) by one female of *T. armigera* as a function of egg density of *H. albipunctella*, *C. cephalonica* and *C. ignefusalis* (no choice condition). For each species, column bearing different letters were significantly different (Student–Newman–Keuls test, α = 0.05).

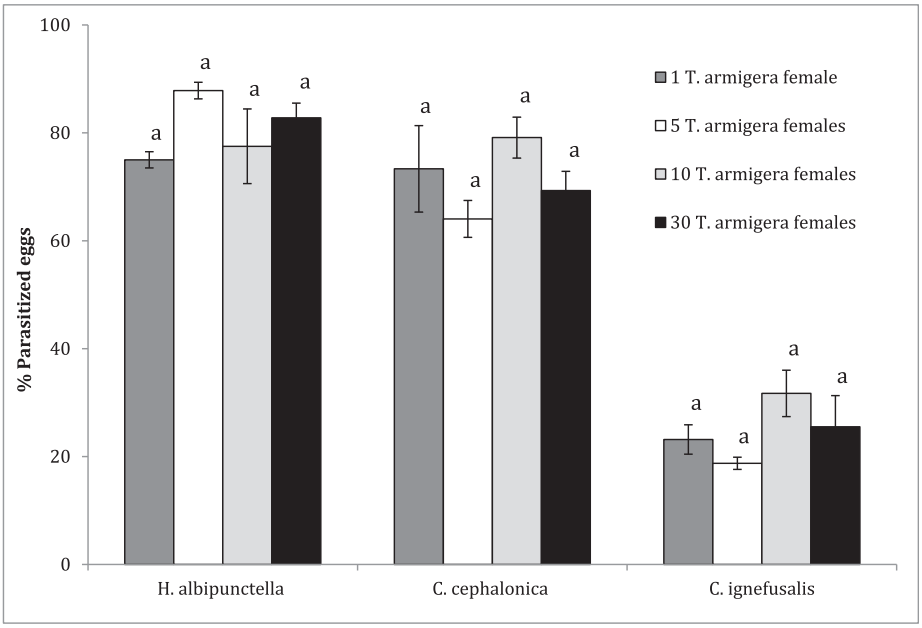

Fig. 4. Parasitism (% ± S.E) of eggs of *H. albipunctella*, *C. cephalonica* and *C. ignefusalis* by *T. armigera* as a function of the number of introduced parasitoids (no choice condition). For each species, column bearing different letters were significantly different (Student–Newman–Keuls test, α = 0.05).

Table 4
Total number of *T. armigera* progeny emerging from 125 eggs of *H. albipunctella*, *C. cephalonica* and *C. ignefusalis* (no choice condition) parasitized by increasing numbers of *T. armigera* females. Within a column, means bearing different letters were significantly different (Student–Newman–Keuls test, α = 0.05).

Number introduced *T. armigera* females	No. emerging *T. armigera* progeny (% ± S.E)		
	H. albipunctella	*C. cephalonica*	*C. ignefusalis*
1	81.50 ± 1.95 ab	46.33 ± 7.68b	4.83 ± 1.54 a
5	86.50 ± 2.86 a	54.58 ± 5.57b	6.00 ± 0.00 a
10	65.33 ± 5.67c	79.66 ± 5.59 a	6.75 ± 0.33 a
30	73.33 ± 2.70 bc	59.83 ± 6.93b	10.50 ± 2.62 a
	$F_{3\text{-}44}$ = 6.71; P = 0.001	$F_{3\text{-}44}$ = 3.87; P = 0.01	$F_{3\text{-}44}$ = 2.54; P = 0.06

of MHM eggs.

In the laboratory, *T. armigera* parasitized a range of lepidopteran species, with preference for *H. albipunctella* and *C. cephalonica*. The average longevity of *T. armigera* females was approximately 12 days, and this is much higher than the average 3–7 days reported in previous studies (Manjunath, 1972; Nagaraja, 1988; Baitha and Ram, 1999). Likewise, in our experiment, the females parasitized many more eggs, and produced 2–5-fold more progeny than previously reported in other settings (Manjunath, 1972; Baitha and Ram, 1999). The difference on *T. armigera* longevity and fecundity may be due to experimental conditions, especially temperature and humidity (Baitha and Ram, 1998, 2001). According to Baitha and Ram (1998), temperature of 25 °C and 30% RH was found most suitable for both *T. armigera* longevity and fecundity. As observed in Indonesia, *T. armigera* has different populations (Bahagiawati et al., 2006) and this could explain differences in life table as reported for other trichogrammatids (Samara et al., 2008; Poorjavad et al., 2011). The development from eggs to adults is completed in 7 days, and this is similar to studies by Manjunath (1972). The mated females produced both sexes in the first 4 days of their life and then only males in subsequent days. This is consistent with the findings of Nagaraja (1988), and it is not surprising as *T. armigera* is an arrhenotokous parthenogenetic species; due in our case to lack of repeated matings, when the stock of sperm is finished, they will produce males only. As a consequence, the overall sex ratio was male-biased, which is contradictory to Manjunath (1972) findings.

Our results indicated that the addition of increasing numbers of *T. armigera* females to a given number of host eggs does not necessarily increase the parasitism. As observed in other settings, the use of excessive numbers of *Trichogramma* could lead to superparasitism (Martel and Boivin, 2004; Reay-Jones et al., 2006) and reduced parasitoid efficiency. As suggested by the egg density study, the proper *T. armigera*: host eggs ratio is 1:30 (6 days parasitism). As a result, for a mass culture of *T. armigera,* one female will have to be given 30 eggs of *C. cephalonica* for parasitism for 6 days and given another batch of 30 eggs for the remaining 6 days of their life. The females will have to be given new males to mate with every 3–4 days for a higher ratio of females in the progeny.

Most parasitoids have the ability to determine host quality during oviposition and will often accept or reject hosts on this basis (Charnov and Skinner, 1985). Overall, our study reveals that *T. armigera* can parasitize all tested species. Of the seven hosts presented to *T. armigera*, the storage pests, *E. kuehniella* and *C. cephalonica*, and the field species, *H. albipunctella* and *H. armigera*, were the most suitable hosts with highest parasitism and parasitoid development. The good performance of *T. armigera* on *H. armigera* confirmed its earlier description as a parasitoid of *H. armigera* in India, Indonesia and Kenya (Manjunath, 1972; Sithanantham et al., 2001; Buchori et al., 2008). *T. armigera* has not been found on eggs of the crambid, *C. ignefusalis*, in the field. Likewise, in the laboratory, *T. armigera* parasitized the eggs of *C. ignefusalis* poorly, and as a consequence, produced limited numbers of progeny. The same observations were made for the other tested crambid species, *N. blitealis.* In Indonesia, in vegetable production, *T. armigera* has been found parasitizing a different range of lepidopteran species from different families, including the crambid species *Crocidolomia pavonana Fabricius* (= *C. binotalis*) (Lepidoptera: Crambidae) and *Scirpophaga incertulas* Walker (Lepidoptera: Crambidae) (Buchori et al., 2008). This indicates that *C. ignefusalis* and *N. blitealis* are not naturally parasitized by *T. armigera* for other reasons than the family of insects to which they belong. The poor development performance of *T. armigera* on eggs of *C. ignefusalis* and *N. blitealis* may be due to their nutritional quality as observed for other trichogrammatid parasitoids species (Spitzen and van Huis, 2005; Kishani et al., 2016). For *C. ignefusalis*, the non-preference for parasitism could be related to the positioning of its eggs on the pearl millet plant. Usually, *C. ignefusalis* deposits its eggs in

the leaf-sheath, which could make them difficult for *T. armigera* to find. However, as observed with the parasitoid *Trichogrammatoidea lutea* Girault, it can parasitize different host-eggs of different species, which are laid on different locations on the host plant. Indeed *T. lutea* is able to search and parasitize both eggs of *Busseola fusca* Fuller (Lepidoptera: Noctuidae) (Sithanantham et al., 2001) and *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) positioned respectively in leaf-sheaths and on the leaf surface of sorghum and maize (Mawela et al., 2013). However, as observed in some *Trichogramma* species (Thorpe, 1985), the searching activity of *T. armigera* could be height specific within the pearl millet canopy, as eggs of *H. albipunctella* are located at the top of the canopy, while those of *C. ignefusalis* are in leaf-sheaths. Moreover, the eggs of both *C. ignefusalis* and *N. blitealis* are ellipsoid compared to the spherical and ovoid shapes of eggs of other tested species. In addition, *C. ignefusalis* eggs are thicker than other tested species, and eggs of *N. blitealis* are translucent. These features could explain the differences in host preference by *T. armigera*. The physical attributes of eggs - size, shape, color and texture – have been reported as selection criteria for parasitism by several trichogrammatid parasitoids (Huang and Gordh, 1998; Cônsoli et al., 1999; Mansfield and Mills, 2002). However, as reported for several trichogrammatids, some chemical features (Frenoy et al., 1992; Schmidt, 1994; Padmavathi and Paul, 1998), or early learning experience (Kaiser et al., 1989; Supoyo et al., 1999; Giunti et al., 2015), could explain the host preference for parasitism by *T. armigera*. Our data suggest that the eggs of *C. ignefusalis* and *N. blitealis* are not suitable for *T. armigera*.

The success of the trichogrammatids in a biological control program is based on their short generation time and high reproductive potential (Pak and Oatman, 1982). In our case, *T. armigera* developed from egg to adult within a period of one week in the lab, which is short enough for population increases, and each female can produce up to 100 progeny, which allows rapid increases of the population. Interestingly, *T. armigera* has easily been reared on the factitious host *C. cephalonica.* This property is particularly important because field releases of parasitoids are not affordable when natural hosts are used in parasitoid mass rearing (Bolckmans, 2003). This finding is indicative of a great potential for use of *T. armigera* in augmentative releases against the MHM. However, compared to the parasitoid *H. hebetor* augmentative program, the challenge with *T. armigera* will be its dispersal in pearl millet fields. As suggested by Michaud (2018), augmentative releases in open environments can be challenging. This could even be more complicated because trichogrammatid parasitoids usually disperse only a few meters from release points (Bueno et al., 2012; Gardner et al., 2012). Augmentation with *T. armigera* will require large numbers of releases in many locations to cover large areas of pearl millet. As for *H. hebetor*, releases of *T. armigera* may be required each growing season, since the survival of the parasitoid in the Sahel could be somewhat challenging due to the unfavorable long dry and hot season (Kabore et al., 2017). But, given that *T. armigera* successfully parasitized *H. armigera,* it could maintain its population on tomatoes during the October-February vegetable production season. On-farm testing will give more indication of the effectiveness of *T. armigera* against the MHM and its survival after releases.

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