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RESEARCH ARTICLE



Field dispersal of the parasitoid wasp *Habrobracon hebetor* (Hymenoptera: Braconidae) following augmentative release against the millet head miner *Heliocheilus albipunctella* (Lepidoptera: Noctuidae) in the Sahel

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ABSTRACT

Pearl millet is one of the major staple food crops in Sub-Saharan Africa, and the millet head miner (MHM) [*Heliocheilus albipunctella*] is its major pest, causing serious economic damage in the maturity period. We studied the dispersion patterns of the endogenous ectoparasitoid, *Habrobracon hebetor* (Hymenoptera: Braconidae), after augmentative releases in pearl millet fields for biological control of the MHM, in 2010 and 2011 in Burkina Faso and Niger. The parasitoids were released using 15 jute bags per release site. Parasitoid dispersion was indirectly monitored through weekly assessments of MHM parasitism by *H. hebetor* at different distances from release points (0, 3 and 5 km) and in control villages (15 km). Our findings indicate that the jute bags released approximately 900–1000 parasitoids per site over a period of three weeks. This initial parasitoid population led to higher parasitism of MHM larvae at the site of dissemination compared to farms at distances of 3 and 5 km. However, usually after five weeks, successive generations of *H. hebetor* dispersed up to 3 km, causing high levels of MHM larval mortality, which sometimes is similar to those of the release points. Based on these results, we recommend the release of parasitoids at sites spaced 3 km for timely and more efficient control of MHM populations.

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Introduction

The millet head miner (MHM), *Heliocheilus albipunctella* de Joannis (Lepidoptera: Noctuidae), is one of the most devastating insect pests of pearl millet (*Pennisetum glaucum*) in the Sahel (Gahukar, 1984). This important univoltine pest has a geographical distribution between latitudes of 11° N and 15° N within the Southern Sahel and Sudan bioclimatic zones (Nwanze & Sivakumar, 1990). The MHM can cause major yield

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losses, especially of early maturing pearl millet (Krall, Youm, & Kogo, 1995; Nwanze & Sivakumar, 1990; Youm & Owusu, 1998). Common pest control methods such as cultural control practices, host plant resistance, and spraying insecticides are ineffective or impractical (Gahukar, 1989, 1990, 1992; Nwanze & Sivakumar, 1990). Biological control has emerged as the most attractive solution for controlling the MHM, and the ectolarval parasitoid *Habrobracon hebetor* Say is considered a natural enemy with a great potential (Gahukar et al., 1986). The effectiveness of this parasitoid against the MHM was first demonstrated in the late 1980s in Senegal (Bhatnagar, 1987, 1989), and subsequently in Niger in the early 2000s (Garba & Gaoh, 2008). In recent years, its effectiveness for augmentative biological control has been demonstrated in the Sahel (Ba et al., 2014, 2013; Kabore, Ba, Dabire-Binso, & Sanon, 2017; Payne et al., 2011), with an estimated yield gain of 34% (Baoua et al., 2014). The parasitoids are released from 15 cm × 25 cm small jute bags containing a mixture of millet grains and flour together with 25 larvae of the rice meal moth, *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae), and two mated *H. hebetor* females (Ba et al., 2014, 2013). Then, two females parasitise the 25 *C. cephalonica* host larvae, and emerging progeny escape through the jute mesh and disperse to parasitize MHM larvae in millet fields (Ba et al., 2014, 2013). Thus, the current release protocol suggests the use of 15 parasitoid bags for coverage of a 5 km² area of pearl millet. This estimate was based on the early recommendations of Garba and Gaoh (2008) but lacked a scientific basis. The release of parasitoids at every 5 km was implemented in our recent work in the region, but evidence of the efficiency of the augmentative biological programme against the MHM was always based on observations made in farms located in villages where parasitoids were released (Ba et al., 2014, 2013).

To succeed in augmentative biological control programmes, it is crucial to understand the number of natural enemies that should be released per area, and knowledge of the mobility and dispersal capacity of *H. hebetor* is essential for the development of appropriate release protocols. The high levels of parasitism resulting from previous studies suggest that the augmentative releases were successful at increasing the degree of mortality by indigenous *H. hebetor*. Understanding how these parasitoids increase and spread can help in understanding factors important to successful biological control through augmentation. In current augmentative programmes, the objective is to quickly reach the MHM larvae before significant crop damages occur; to accomplish this, the *H. hebetor* parasitoids must disperse from the release points and spread throughout the infested area. To rationalise the current biological control programmes, it is crucial to not only have empirical estimates of the number of *H. hebetor* to be released but also to know how many sites per release area should be considered. The aim of this work was to evaluate the dispersal ability of released *H. hebetor* adults and parasitism rates of MHM after augmentative release and to determine the release protocol that provides the highest parasitoid efficiency.

Materials and methods

Study location

The experimental trials were conducted in typical pearl millet production areas of the Sahel agroecological zone of Burkina Faso and Niger in 2010 and 2011. This agroecosystem has a unimodal rainfall pattern with the rainy season extending from June to October,

and annual rainfall varying between 450 and 550 mm. The maximum relative humidity reaches 92% during the millet season, and temperatures range from 24°C to 39°C during the rainy season. During this period, the area has continuous pearl millet fields covering almost 80% of the cultivated area usually in association with cowpea, while uncultivated land is left for grazing livestock. Farmers grow 2–3 local pearl millet varieties planted in May–June at densities ranging from 4000 to 6000 plants/hills per ha on 3–10 ha. No irrigation or chemical fertiliser is applied to any of the fields.

Parasitoid rearing

A *H. hebetor* colony was established from field-collected MHM larvae and maintained in the laboratory at room temperature (mean = $26 \pm 2^\circ\text{C}$) on the rice meal moth, *C. cephalonica*, at the National Agricultural Research Institutes of Burkina Faso and Niger. Field-caught insects were added to the colonies once per year. Rice moths were reared on a mixture of pearl millet grain and flour in wooden cages (20 × 20 × 13 cm), and the parasitoids were reared on third and fourth instar *C. cephalonica* larvae using a technique described by Ba et al. (2014, 2013).

Assessing initial numbers of parasitoids emerging from bags placed in millet fields

This experiment was carried out in 2010 and included 6 villages in each country, each supplied with 10 parasitoid jute bags (25 cm × 15 cm). Each parasitoid bag contained 500 g of millet, 25 *C. cephalonica* larvae and two mated *H. hebetor* females. The parasitoid-containing bags were placed within millet farms (2 bags/farm) and covered with muslin cloth to trap the emerging parasitoids. Bags were kept in the field for 1 month, and emerging parasitoids were sexed, counted and removed daily.

Based on the initial number of parasitoid-inoculated hosts from each bag, we estimated the population of *H. hebetor* build-up over the four weeks in the field using the published *H. hebetor* life tables on MHM larvae (Youm & Gilstrap, 1993a). The same data were used to estimate the total MHM larvae population killed/parasitised.

Assessing field dispersal of parasitoids after on-farm releases

This experiment was carried out in 2010 with a group of four villages in Burkina Faso and four villages in Niger selected for endemic infestations with the MHM with over 60% of panicles infested. In each country, the four villages were located at least 25 km apart. Each of the four villages was supplied with 15 parasitoid bags as described above, evenly distributed among five millet farms (three bags/farm) using methods described by Ba et al. (2014). Dispersal of parasitoids was monitored from release points following transects in wind and crosswind directions. Observation points were located at farms 0 km and 3 km from parasitoid release points and in control, no-release villages located 15 km away from release points.

At each observation point, 200 pearl millet panicles were randomly collected. The data were collected weekly, starting on the day of parasitoid bag establishment and ending five weeks later. Parasitoid dispersal was indirectly assessed by counting the numbers of live

(unparasitised) and *H. hebetor*-parasitised MHM larvae. Larvae parasitised by *H. hebetor* were easily distinguished by the presence of cocoons (Garba & Gaoh, 2008).

The same experiment was repeated in 2011 in another set of four villages in Burkina Faso and Niger. The villages were selected using some of the characteristics listed above. In this experiment, the parasitoids were released in each of the four villages, and dispersal of parasitoids was monitored at 0, 3 and 5 km from release villages and in control villages located 15 km away from release points using the methods described above.

Data analysis

Data for MHM parasitism by *H. hebetor* in wind and crosswind directions was pulled for each location and compared using Analysis of Variance (ANOVA PROC GLM) with SAS software version 9.1 (SAS, 2003). When ANOVAs were significant, means were compared by the Student–Newman–Keuls tests at the 5% level. Percentages from parasitism data were arcsine transformed prior to statistical tests.

Results

Parasitoid emergence from jute bags

When parasitoid bags were deployed on the millet farms, the parasitoid progeny began emerging from the bags 8 days after confinement of *H. hebetor* females with *C. cephalonica* larvae. The emergence period lasted 7 days in Burkina Faso, while it extended to 12 days in Niger (Figure 1). Up to 70 parasitoids emerged from the bags in Burkina Faso, while only 60 emerged from the bags in Niger. The emerging parasitoids had a sex ratio of 0.72 (female/male) in Burkina Faso and 0.57 (female/male) in Niger. The estimated numbers

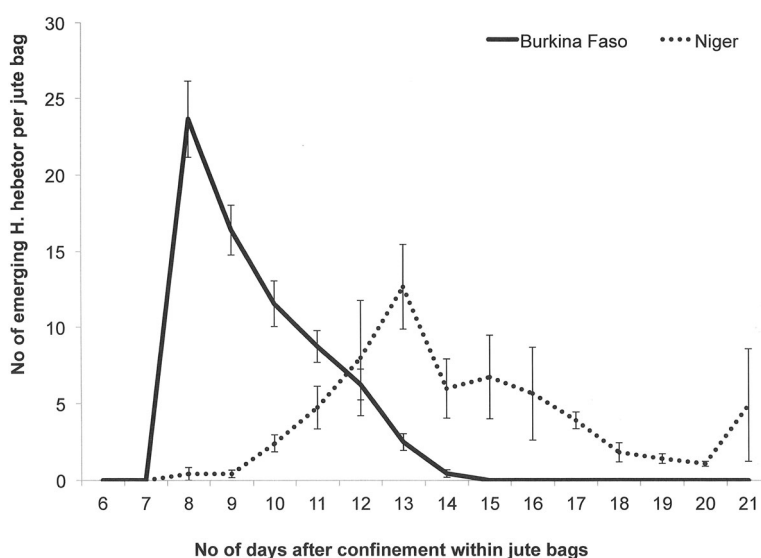


Figure 1. Daily emergence of *Habrobracon hebetor* (Say) (mean ± SE) from jute bags deployed in pearl millet fields in Burkina Faso and Niger.

of *H. hebetor* female population build-up from the inoculum ranged between 960,000 and 1.4 million after one and half months (Figure 2). This led to a cumulative parasitisation of potentially 465,000–697,000 MHM larvae (Figure 2).

Parasitism of the MHM with *H. hebetor*

In Burkina Faso in 2010, parasitism of the MHM by *H. hebetor* was first observed at experimental sites two weeks after parasitoid bags were deployed (Figure 3(a)). Parasitism was observed one week later at the 3 and 15 km control sites but with a significantly lower level of parasitism ($F_{2, 592} = 64.69$, $P < .0001$; Figure 3(a)). Similarly, four weeks after parasitoid bags were deployed, the level of parasitism of the MHM by *H. hebetor* remained significantly higher ($F_{2, 554} = 61.02$, $P < .0001$) at the release site, and the 3 km locations had significantly higher parasitism than the control located 15 km away from the release sites (Figure 3(a)). The same trend was observed 35 days post releases ($F_{2, 607} = 77.56$, $P < .0001$; Figure 3(a)).

In Niger in 2010, parasitism was observed at all distances 14 days after parasitoid bags were deployed, but with a significantly higher level of parasitism at the release sites ($F_{3, 596} = 14.81$; $P < .00001$; Figure 3(b)). The same trend was observed 21 days post-parasitoid deployment ($F_{3, 596} = 28.40$; $P < .00001$; Figure 3(b)). However, after 28 days, sites at both 0 and 3 km distance from the release sites had a similar level of MHM parasitism with *H. hebetor*, and these sites had higher parasitism rates than the control ($F_{3, 796} = 312.93$; $P < .00001$; Figure 3(b)).

In Burkina Faso in 2011, parasitism of the MHM by *H. hebetor* was observed 14 days after parasitoid bags were deployed in millet farms, with significantly higher parasitism in villages located at the release sites ($F_{3, 490} = 17.22$, $P < .0001$; Figure 4(a)). Parasitism increased over the weeks at all locations and remained significantly higher at release sites after 21 days ($F_{3, 1077} = 44.52$, $P < .0001$; Figure 4(a)) and 28 days ($F_{3, 1111} = 39.00$, $P < .0001$; Figure 4(a)). At the end of the season, all villages located up to 3 km from

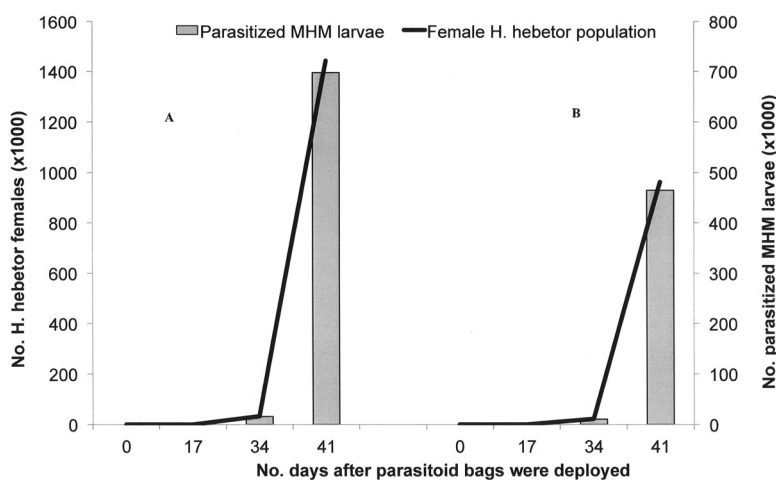


Figure 2. Projected numbers of *Habrobracon hebetor* (Say) population after augmentative releases and corresponding number of parasitised millet head miner (MHM) larvae in pearl millet fields in Burkina Faso (A) and Niger (B).

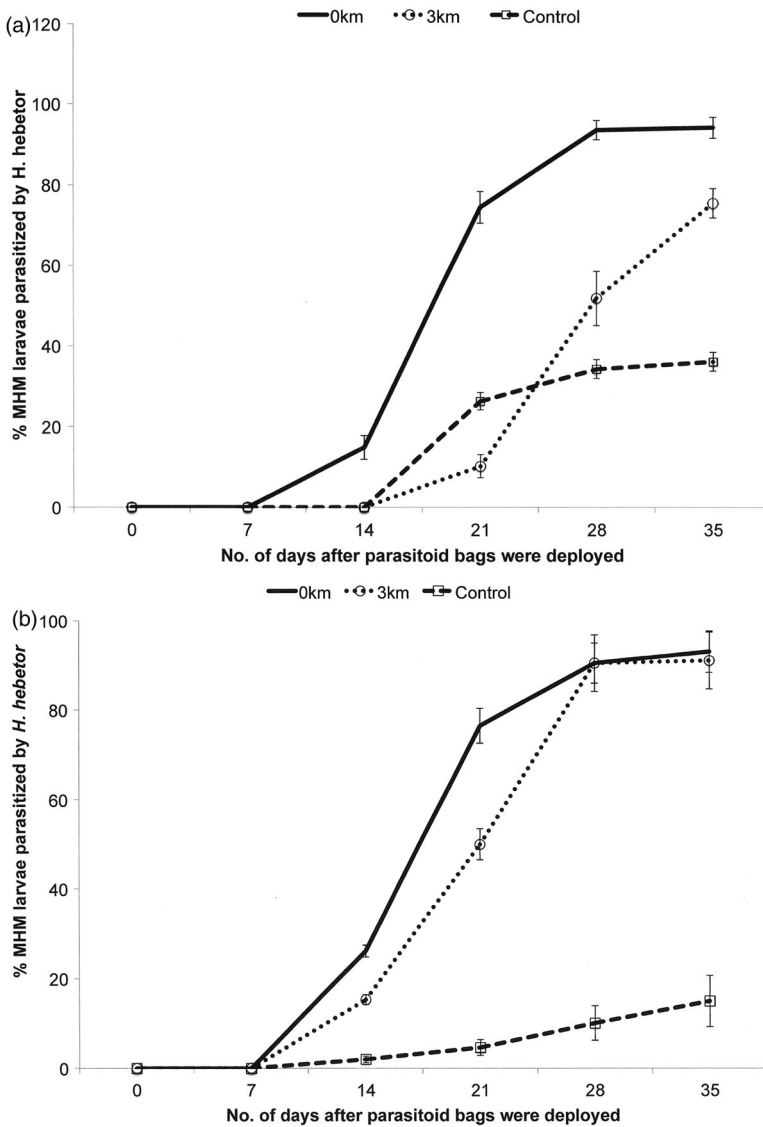


Figure 3. Parasitised larvae of millet head miner (MHM), *H. albipunctella* (% mean \pm SE) due to *H. hebetor* at a different distance from release sites and control villages after augmentative releases of *H. hebetor* in 2010 in (a) Burkina Faso and (b) Niger. (For each date, means were compared by a Student–Newman–Keuls test at the 5% level.)

parasitoid release sites had over 50% levels of parasitism and remained significantly higher than the 5- and 15-km control ($F_{3, 815} = 56.21$, $P < .0001$; Figure 4(a)).

In Niger in 2011, parasitism was also first recorded two weeks after parasitoid bags were deployed in millet farms, with significantly higher parasitism at release villages ($F_{3, 596} = 30.08$, $P < .00001$; Figure 4(b)). From three weeks after release onward, similar levels of parasitism were recorded at the 0 and 3 km distances, but levels were significantly higher at these sites than at the 5 km and control sites (three weeks: $F_{3, 596} = 4.65$, $P = .003$; four weeks: $F_{3, 1196} = 7.23$; $P < .0001$; Figure 4(b)).

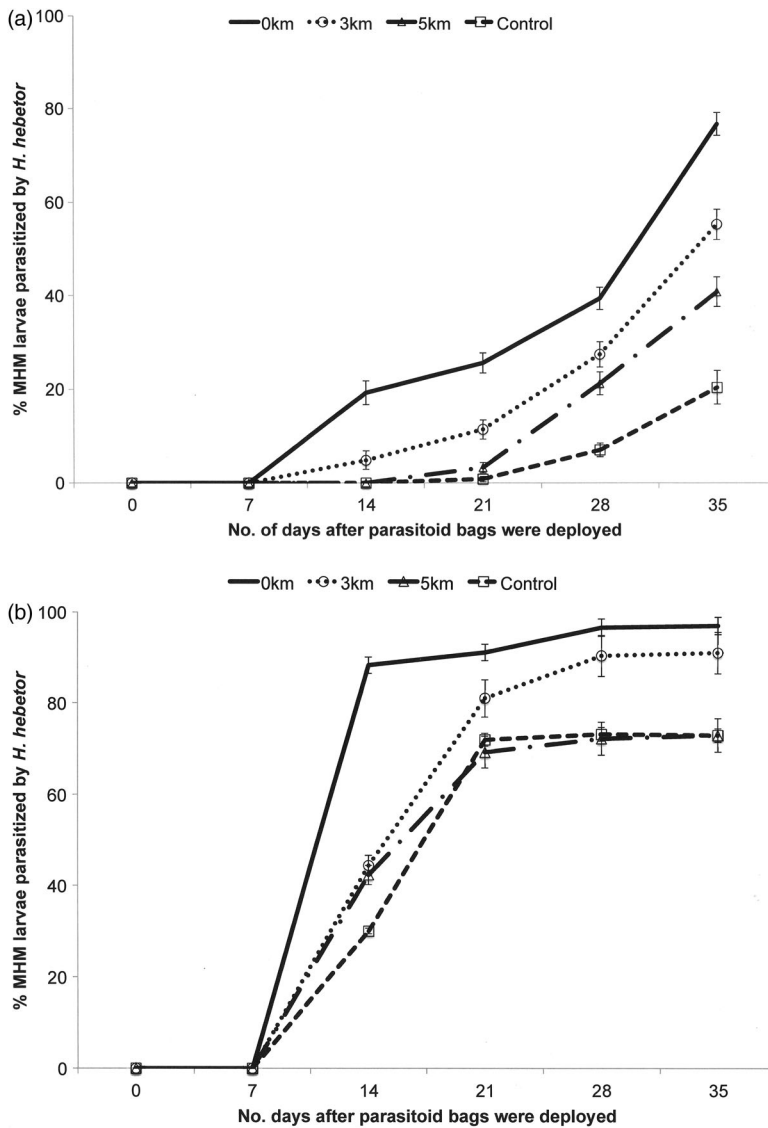


Figure 4. Parasitised larvae of millet head miner (MHM), *H. albipunctella* (% mean \pm SE) due to *H. hebetor* at a different distance from release sites and control villages after augmentative releases of *H. hebetor* in 2011 in (a) Burkina Faso and (b) Niger. (For each date, means were compared by a Student–Newman–Keuls test at the 5% level.)

Discussion

In this study, dispersal of the MHM parasitoid *H. hebetor* was evaluated in the field after augmentative releases. The parasitoid started emerging from the jute bags one week after being deployed in farmer fields, and each bag delivered 60–70 offspring. This is consistent with previous lab data on parasitoid emergence from jute bags (Ba et al., 2014). The initial population of 60–70 parasitoids per bag corresponds to approximately 900–1000 per release. Based on published life table data of *H. hebetor* (Youm & Gilstrap, 1993a), this

initial inoculum could lead to an estimated 1.4 million progenies after one and a half months. This numbers should, however, be lowered because as reported in other settings parasitoid wasps may face predation of generalist predators (Heimpel, Rosenheim, & Mangel, 1997; Snyder & Ives, 2001; Traugott, Bell, Raso, Sint, & Symondson, 2012). Moreover, the few insecticides sprayed on cowpea (Murdock et al., 2008), which is usually intercropped with pearl millet, can also reduce parasitoids population. Such mortality can hamper the parasitism achieved by released *H. hebetor*, hence reducing the efficacy of augmentative biological control. However, our field data indicate high mortality of the MHM due to *H. hebetor* suggesting limited mortality of *H. hebetor* over the cropping season.

Indeed in both countries, and for both 2010 and 2011 years, on-farm parasitism of the MHM by *H. hebetor* was recorded one week after parasitoids began emerging from jute bags (i.e. 14 days after bags were placed). Parasitism increased steadily over the five weeks, with significantly higher parasitism rates in farms located at release sites. However, after 3–4 weeks, very high levels of parasitism were found at all locations up to 3 km from release points. Usually after 4–5 weeks, parasitism at villages 5 km from the release sites also reached high levels, but these levels were still lower than levels at the points of release. Parasitoid flight distance varies among species and ecological habits. Trichogrammatidae, for example, usually disperse only a few metres from release points (Bueno, Parra, & Bueno, 2012; Gardner, Wright, Kuhar, Pitcher, & Hoffmann, 2012). Other parasitoid species may disperse only a few metres from release points (Evans, Bolshakova, & Carlile, 2015; Zappala et al., 2012) to a few kilometres (Grillenberger, Gadau, Bijlsma, Van De Zande, & Beukeboom, 2009). In Brazil, the related Braconidae species, *Diachasmimorpha longicaudata*, has also been found dispersing lesser distances in coffee plantations (Camargos et al., 2016), while another braconidae species, *Microplitis mediator* (Haliday), was found to fly a distance of 6–18 km in just a few hours (Yu, Zhang, Wu, Wyckhuys, & Guo, 2009). In the USA, the related *Peristenus* braconid parasitoid was found to travel 16–18 km per year after introduced releases (Day, Tilmon, Romig, Eaton, & Murray, 2000; Pickett et al., 2013).

Most studies of *H. hebetor* refer to insect pests of stored commodities (Ghimire & Phillips, 2010). Apart from the ongoing work on the use of *H. hebetor* against the MHM in the Sahel (Ba et al., 2014, 2013; Baoua et al., 2014; Kabore et al., 2017), outdoor releases of *H. hebetor* are quite rare, with only a few cases reported in Iran against *Helicoverpa armigera* larvae in cotton fields (Navaei, Taghizadeh, Javanmoghaddam, Oskoo, & Attaran, 2002) and in India for the suppression of coconut head caterpillar *Opisina arenosella* (Desai, Nagwekar, Patil, & Narangalkar, 2007; Mohanty et al., 2000). Unfortunately, none of those reports investigated field dispersal of *H. hebetor* after release. To our knowledge, the only available study on field dispersal of *H. hebetor* reported a 1 km dispersal from the release point after 6 days in a tomato field in Russia (Adashkevich, Saidova, & Takanaev, 1986). This 1 km dispersal distance is, however, shorter than the 3–5 km distance found in the current study. This could be due to differences in methodology as Adashkevich et al. (1986) investigated *H. hebetor* dispersal after only 6 days of observations while in the present study *H. hebetor* dispersal was monitored for 5 weeks. Moreover, as reported in other settings, parasitoid species dispersal distance could be influenced by weather, especially temperature (Fahrner, Lelito, & Aukema, 2015; Yu et al., 2009), wind (Desouhant, Driessen, Lapchin, Wielaard, & Bernstein, 2003; Kristensen, Schellhorn, Hulthen, Howie, & Barro, 2013; Messing, Klungness, & Purcell, 1994) and landscape (Josso et al., 2013).

As *H. hebetor* is endemic to the Sahel region (Bhatnagar, 1987; Gahukar et al., 1986; Nwanze & Harris, 1992), the effects of our releases could only be compared to control sites (i.e. 15 km distance), which had similar levels of MHM infestation, and are not subjected to augmentative releases. Differences in levels of parasitism, especially recorded early in the season, could then be attributed to our augmentative releases. *H. hebetor* naturally parasitises the MHM at rates ranging from 2% to 95%, but often towards the end of the season after the crop has been damaged (Bhatnagar, 1989; Gahukar et al., 1986; Youm & Gilstrap, 1993b). In our case, there is strong evidence of the rapid spread of *H. hebetor* in pearl millet field, covering a radius of 3 km. However, comparable levels of MHM parasitism with *H. hebetor* were also observed at farther distances (3–5 km) from release points 3–5 weeks after releases were made. Since *H. hebetor* has a rapid developmental time and a high rate of population growth (Magro & Parra, 2001; Nikam & Pawar, 1993), about three generations could develop on larvae of MHM within 7 weeks. This suggests that dispersal of the parasitoid up to 5 km occurred over several generations, with successive *H. hebetor* generations colonising additional areas. A similar observation was made in Ireland with the Encyrtidae parasitoid wasp, *Psyllaephagus pilosus* (Noyes), on the psyllid host, *Ctenarytaina eucalypti* (Maskell), in eucalyptus plantations, in which successive generations of the parasitoid spread to up 70 km from the release point after only 5 months (Chauzat, Purvis, & Dunne, 2002). The context is different in the Sahel as the host species, *H. albipunctella*, develops only during the rainy season and remains in diapause for more than 10 months (Gahukar et al., 1986). *H. hebetor* thus has limited options for survival during the off-season (Kabore et al., 2017).

Parasitoid dispersal is typically density dependent (Antolin & Strong, 1987). In our case, however, MHM host density was uniform over the area with an estimate of at least 60% infestation of pearl millet panicles. The village 5 km away from the release site was reached by the parasitoid almost toward the end of the season. Our findings confirm the effectiveness of augmentative releases of *H. hebetor* for controlling the MHM in the Sahel (Ba et al., 2014, 2013; Baoua et al., 2014; Kabore et al., 2017). As shown in our study, parasitism of MHM larvae by *H. hebetor* increases over several weeks, and the parasitism rates at points of release were much higher than all other distances, with a 1.27–6.20-fold increase in control as observed previously (Ba et al., 2014, 2013).

We were also able to document the seasonal variability of the parasitism at different distances from release points, which was missing in the Garba and Gaoh (2008) study. Our findings clearly demonstrate that the end of seasonal parasitism at 5 km never reached the level observed at the point of parasitoid releases. The Garba and Gaoh (2008) 5 km dispersal distance was based on observations made 30 days after parasitoid releases and lack control villages. As indicated earlier, *H. hebetor* had endemic presence in the region and, as reported by Gahukar et al. (1986), *H. hebetor* is active mainly towards the end of the crop season. For this reason, unless compared with a control, it is not accurate to only attribute the parasitism at 5 km distance to the augmentative releases but rather to a cumulative effect of natural and augmentation. The formulation of 15 bags per village seems to be appropriate for reducing the pest population at the distance of 3 km. At 5 km distance, the high level of mortality was found only at the end of the season, which will not provide acceptable control of MHM. For the highest and timely control of the MHM, we suggest the release of parasitoids every 3 km. Since production of parasitoids and release efforts may be economically challenging, releases every 5 km could

be used especially for resource-poor communities. Direct release of adult wasps could be investigated to potentially avoid the two-week delay in parasitoid dispersal that results from rearing them in bags; or bags could be deployed two weeks earlier than the required release. Similarly, the number of parasitoids to be released per area needs further investigation.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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