

Old and new association of *Cotesia icipe* (Hymenoptera: Braconidae) with alien invasive and native *Spodoptera* species and key stemborer species: implication for their management

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Abstract

BACKGROUND: Maize production in Africa is hindered by a myriad of biotic challenges, key among them being invasive and native lepidopteran stemborers. Recent invasion of the continent by fall armyworm, *Spodoptera frugiperda*, has further exacerbated the situation. Fortunately, *Cotesia icipe* was found to be very promising against *S. frugiperda*. However, the co-occurrence and interaction between *S. frugiperda* and the stemborers (*Busseola fusca*, *Sesamia calamistis*, and *Chilo partellus*) in maize agroecosystem may jeopardize the efficiency of *C. icipe* as a biocontrol agent of *S. frugiperda*. This study investigated the performance of *C. icipe* on *S. frugiperda*, *Spodoptera littoralis* and the stemborers. Specifically, the preference and acceptability of *C. icipe* to the host insects, the physiological suitability of the hosts for its development, and the effect of these hosts on the fitness parameters of the offspring were assessed.

RESULTS: *Cotesia icipe* accepted all the tested hosts, albeit with higher preference for *Spodoptera* species than for stemborers under multiple-choice tests. Also, the highest parasitism of up to 97% was recorded on *S. frugiperda* compared with parasitism on the stemborers of 43% in *B. fusca*. Moreover, physiological suitability and fitness traits (except for per cent female offspring) varied with host species, again being optimal on *Spodoptera* species.

CONCLUSION: *Cotesia icipe* demonstrated strong potential to control *S. frugiperda* in maize due to its high affinity for parasitization and developmental success in this host; and despite its non-specific parasitization, the presence of other hosts may not prevent its maximum control of *S. frugiperda*.

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Keywords: biological control; parasitoid host range; invasive pest; fall armyworm; maize agroecosystem

1 INTRODUCTION

The production of maize, *Zea mays* L. (Poaceae) in sub-Saharan Africa is hampered by a myriad of biotic and abiotic challenges. Among the biotic factors, lepidopteran pests such as native stemborer species, *Sesamia calamistis* Hampson and *Busseola fusca* (Fuller) (both Lepidoptera: Noctuidae), and invasive stemborer, *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae), are major pests of maize.^{1–4} For example, maize yield losses due to infestation by these pests has been estimated to be 12.9% in Kenya⁵ and up to 50% in Mozambique.⁶ The invasion of the African continent by the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) from the Americas in 2016,⁷ further compounded the problem, with an estimated additional annual maize yield loss at USD 9.4 billion from *S. frugiperda* alone.⁸

Largely, synthetic pesticides are used for the control of *S. frugiperda* in Africa.⁹ The use of pesticides can reduce invasive

pest incidence, but the injudicious use of broad spectrum chemical pesticides is detrimental to human, animal and environmental health (One Health).^{10,11} An overreliance on chemical insecticides often leads to the development of resistance by the target pest(s). Indeed, insecticide resistance in *S. frugiperda* populations has been reported widely in its native range¹² and more recently in its invasion regions in Africa, Asia and Australia.^{13–17} The resistance to

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variety of insecticide classes (e.g. organophosphates, spinosyn and carbamates, among others) by the pest, results from its genetic plasticity and high fecundity, as well as intense selection pressure.¹⁸ Overall, overreliance on synthetic pesticides as the only management approach is untenable.¹¹ Thus, there is need for the development and adoption of other sustainable approaches within the framework of integrated pest management (IPM) for suppression of the lepidopteran pests in maize cropping system.

Within the IPM approach, several strategies such as early monitoring, cultural practices, physical control and biological control have been employed for management of *S. frugiperda*.^{19–21} Biological control using parasitoids represents a good option for management of invasive pests. This approach involves three strategies: classical, augmentative and conservation biocontrol. Sometimes the three strategies are not mutually exclusive. Across the native range of *S. frugiperda*, the dominant parasitoid that has been recorded is the egg-larval parasitoid, *Chelonus insularis*, (Cresson) (Hymenoptera: Braconidae), together with other larval parasitoids such as *Campoplex sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) and *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae).²² However, for the augmentative biocontrol of the pest, *Telenomus remus* Nixon (Hymenoptera: Platygasteridae) and *Trichogramma* spp. have been used in the Americas.¹⁹ Following the pest's detection and rapid spread in Africa, several egg parasitoids, e.g. *T. remus*, *Trichogramma chilonis* Ishii and *Trichogramma mwazaii* sp. n. (both Hymenoptera: Trichogrammatidae),^{23,24} and larval parasitoids have been reported on fall armyworm across Africa and Asia.¹⁹ Among the larval parasitoids, *Cotesia icipe* Fernández-Triana & Fiaboe (Hymenoptera: Braconidae), a solitary koinobiont larval parasitoid of *Spodoptera littoralis* (Boisduval) and *Spodoptera exigua* (Hübner) (all Lepidoptera: Noctuidae),^{25,26} has been found to be a promising parasitoid of *S. frugiperda*.^{24,27,28} However, the co-occurrence and interaction between *S. frugiperda* and the stem-borers (*S. calamistis*, *B. fusca*, *C. partellus*), as well other defoliators such as *S. littoralis* and *Spodoptera exempta* (Scott) (Lepidoptera: Noctuidae), which occupy the same agroecological zone or occur on the same host plant,^{27,29,30} may have diverse implications for the efficiency of *C. icipe* as a biocontrol agent of *S. frugiperda*. In this regard, there is a need to investigate possibility of the parasitoid's new association with stem-borers, as well as its performance on the target pest (*S. frugiperda*), in the presence or absence of other known (*S. littoralis*) and potential hosts (stem-borers). Therefore, in this study, we: (i) assessed the preference and acceptability of *C. icipe* to *S. frugiperda*, *S. littoralis*, *B. fusca*, *S. calamistis*, and *C. partellus*; (ii) determined the physiological suitability of these hosts for the development of the immature stages of the parasitoid; and (iii) assessed the effect of the host larvae on fitness parameters of the parasitoid offspring.

2 MATERIALS AND METHODS

2.1 Host plants

Maize, *Zea mays* L. (Poaceae) and *Amaranthus viridis* L. (Amaranthaceae) were grown in insect-proof greenhouses. Two seeds of the plants were sown directly in 2-L plastic pots, half-filled with red soil mixed with goat manure (ratio 2:1), and the seedlings were maintained without application of fertilizers or chemicals. Plants about 4–6 weeks old were used in the study.

2.2 Host insect

Stemborer populations were obtained from a laboratory colony maintained at the Animal Rearing and Containment Unit (ARCU)

of International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya. The larvae were reared on artificial diet according to the methods described by Ochieng *et al.*³¹ for rearing of *C. partellus*, and Onyango and Ochieng'-Odero³² for rearing of *B. fusca* and *S. calamistis*. In brief, stem-borer eggs were collected from oviposition cages, then placed in 2-L transparent plastic jars lined with moistened paper towel until they hatched. First-instar larvae were introduced to freshly prepared artificial diet, allowed to develop in the diet and then used in the bioassays.

Initial field samples of *S. frugiperda* and *S. littoralis* were collected from Yatta (Machakos County; 01.23044° S, 37.45789° E) and Mwea Irrigation Scheme (Kirinyaga County; 0.6309° S, 37.35117° E). They were maintained on artificial diet formulated at the *icipe* laboratory³³ and reared at the ARCU for three filial generations before commencement of the bioassay. All insects used in the bioassays were kept under laboratory conditions of 25 ± 2 °C, 70% ± 5% relative humidity (RH) and a 12:12 h light/dark photoperiod.

2.3 Parasitoid colony

Cotesia icipe wasps used in study were obtained from *icipe*'s laboratory culture at the ARCU, where the parasitoid was reared on *S. frugiperda* for more than eight generations according to the method described by Mohamed *et al.*²⁸ In brief, second-instar larvae of *S. frugiperda* on pieces of maize leaf were placed in 1-L plastic jars. The jar was then placed in a Perspex cage (40 × 40 × 20 cm) holding mated female *C. icipe* for parasitization over a period of 24 h. Parasitized larvae were then transferred to plastic boxes and maintained on maize leaves until cocoon formation in the laboratory at 25 ± 2 °C, 70% ± 5% RH and a 12:12 h light/dark photoperiod. Cocoons were collected, placed in Petri dishes and introduced into clean Perspex cages for wasp eclosion. Eclosed wasps were fed on natural honey and provided with water in the form of moistened cotton wool.

2.4 Bioassays

2.4.1 Host preference by *C. icipe*

The host preference of *C. icipe* was measured in two regimes under multiple-choice test: (i) dissecting individual larvae of the tested host insects after exposure to parasitoids; and (ii) the number of wasps searching and/or ovipositing in the larvae of host insects. Observation of the number of wasps searching and/or ovipositing was used as a proxy for the preference test. These tests were conducted simultaneously, with the proportion of wasps that sought and/or oviposited in the larvae recorded on the day of experiment, and the number of parasitized larvae of the different host species counted exactly 1 day after termination of the bioassay.

To perform the bioassay, a clean Perspex cage (40 × 40 × 20 cm) holding a small moistened cotton wool ball as a water source and streaks of natural honey carefully placed on the upper underside of the cage as a food source, was prepared as the experimental unit. Five jars holding fresh and young maize leaves in case of stem-borers and *S. frugiperda*, and amaranth leaves for *S. littoralis* were prepared and clearly labelled. Twenty first-instar larvae of the tested host insects were transferred to the jars, which were placed in the Perspex cage in an 'X' pattern (~13 cm apart). This pattern was used to avoid position bias of the jars during the replications of the experiment. The bioassay was replicated ten times, whereby for each replicate, jars holding a particular host insect occupied different positions in the 'X' pattern. Five 2-day-old mated but naïve *C. icipe* wasps were aspirated into vials, then transferred to the Perspex cages by placing the vial at the bottom centre of the cage;

parasitoids were allowed to fly freely out of the vials. To score host searching and/or oviposition by *C. icipe*, throughout the 90-min exposure of the host larvae to the parasitoid, the number of parasitoids in the different jars (each jar held different host species) were observed and recorded at 10-min intervals. After the 90-min recording period, the parasitoids were allowed to continue parasitizing the larvae for a further 3 h, without recording their activity. The experiment was then terminated, with all wasps aspirated out of the experimental unit; larvae of the different host species were maintained separately in the jars. All the exposed larvae were dissected under a stereomicroscope [Leica Microsystems (Heerbrugg, Switzerland) integrated with digital cameras and operated using a Leica Application Suite (LAS) Microsystem] 24 h after termination of the experiment. The average number of parasitized larvae from each host species, for all the ten replicates, was calculated and used in a confirmatory assessment of the preference.

2.4.2 Host acceptability by *C. icipe*

Host acceptability was defined by the presence of *C. icipe* eggs in the host larvae. The acceptance of *C. partellus*, *B. fusca*, *S. calamistis*, *S. frugiperda* and *S. littoralis* by *C. icipe* was evaluated in a no-choice experiment. In a similar way as described for preference test, 20 first-instar larvae of each host insect were placed individually in a 1-L transparent plastic jar holding plant leaves. The jars with the insect larvae were then placed in clean Perspex cages (20 × 20 × 20 cm) that were also prepared in a way similar to those described for the preference test. In each cage, one mated but naïve *C. icipe* female wasp was then introduced and allowed to oviposit into the host larvae for 8 h, after which the individual jars were removed from the cages and closed with a netted lid. Within 24 h post-oviposition, all the larvae were removed and dissected under stereomicroscope [Leica Microsystems (Heerbrugg, Switzerland) integrated with digital cameras and operated by Leica Application Suite (LAS) Microsystem]. The number of parasitized larvae and number of parasitoid eggs per larvae were counted and recorded. The experiment was replicated ten times for each host species.

2.4.3 Host physiological suitability for *C. icipe* offspring development

To evaluate host suitability, the following parameters were assessed: developmental time of parasitoid immature stages (egg and larva), and from cocoon formation to wasp eclosion; number of cocoons formed; number of eclosed wasps; and host immune response in terms of encapsulation/melanization. In a no-choice test, first instars ($n = 40$) of each host species were exposed to four (1:1 female to male ratio) 2-day-old naïve mated *C. icipe* wasps for 8 h in a similar way to that described above for the host acceptability test. Upon termination of the experiment, and after 24 and 36 h, ten larvae for all host species were randomly picked and dissected under the stereomicroscope, and the egg incubation period of *C. icipe* across all the host species was recorded. In cases in which more than one parasitoid egg was deposited, the developmental duration for the older stage of the parasitoid was scored. The remaining 20 larvae were maintained on their respective host plants for further development. Times to cocoon formation and adult eclosion were monitored and recorded. Unparasitized larvae were excluded from the analyses. Further, the number of cocoons formed and number of eclosed wasps were recorded.

To assess the host immune response to the parasitoid attack, the encapsulation rate of *C. icipe* was recorded in each parasitized

host species. Sixty first-instar larvae of each host species were exposed to three female *C. icipe* and the parasitoid was allowed to oviposit in the host for 8 h. After 24, 36 and 48 h post-parasitization, 20 larvae were randomly picked from the parasitized cohort and dissected under the stereomicroscope to assess for encapsulation or melanization of parasitoid eggs.

2.4.4 Effect of the rearing host on fitness parameters of *C. icipe*

Effect of the rearing host on *C. icipe* fitness was measured in terms of percentage cocoon formation, sex ratio, body size and longevity of parasitoid offspring. In a no-choice test, a set of 20 first-instar larvae of each host species were transferred to a transparent 1-L plastic jar holding pieces of their respective host plants. The jar was then transferred to a Perspex cage (20 × 20 × 20 cm) with honey streaks on the upper underside of the cage. A pair (one female and one male) of 2-day-old *C. icipe* wasps were then aspirated into the experimental cage and allowed to parasitize the host larvae for 8 h, after which the parasitized larvae were individually transferred to their respective artificial diet (prepared in glass specimen tubes; 75 × 25 mm soda glass poly stopper) and maintained under ambient laboratory conditions until cocoon formation. The number of formed cocoons was recorded and cocoons were allowed to develop in their respective vials until wasp eclosion. The number of eclosed wasps and their sex ratio were then recorded. Female wasps that emerged from each host insect were dissected individually under the stereomicroscope and left forewing length and width, as well as the length of the left hind tibia were measured to assess the effect of host species on wasp body size.

To assess the longevity of the wasps reared on different host species' larvae, a set of 15 newly emerged naïve *C. icipe* females and males for each host species were maintained separately in Perspex cages (20 × 20 × 20 cm) under ambient laboratory conditions and provided with food and water as described for parasitoid rearing. Mortality was monitored and the number of the dead wasps was recorded daily at 18:00 until all wasps died.

2.5 Data analysis

All statistical analyses were performed using R.³⁴ The data for host acceptability (number of parasitoid eggs per larvae) and preference (number of responding wasps); host suitability (estimated based on the rate of cocoon formation and further expressed as the percent parasitism); wasp eclosion (measured as the total number of wasp regardless of sex); sex ratio (measured as the proportion of females); developmental time of the immature stages; and fitness of the wasps (only for the morphological fitness) were subjected to normality test using the Shapiro–Wilk test, followed by one-way analysis of variance (ANOVA). Log transformation (log +1) was used for data that were not normally distributed before performing a one-way ANOVA test. Where significant differences were detected ($P < 0.05$), data were subjected to the Student–Newman–Keuls method ($\alpha = 0.05$) for means separation. Further, the effect of host species on the longevity of *C. icipe* progenies was analysed by one-way ANOVA, whereas *t*-test ($P < 0.05$) was used to compare the longevity for different sexes reared on the same host species.

3 RESULTS

3.1 Host preference of *C. icipe*

The number of *C. icipe* wasps recorded as searching and/or ovipositing (the scoring used in this study as a proxy to assess the host preference) varied significantly among the host species

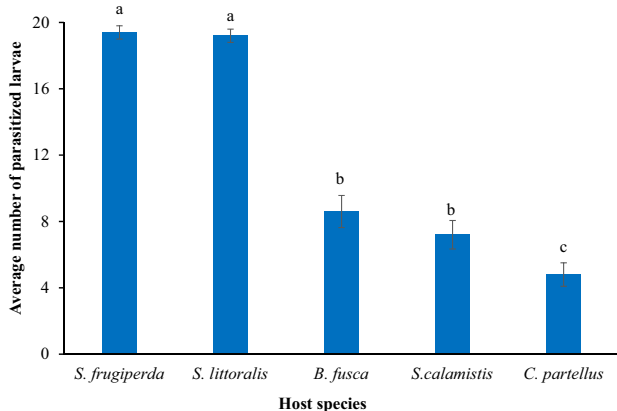


Figure 1. Average number of parasitized larvae under a multiple-choice test scenario. Means with same letters indicate that the number of parasitized host larvae is not statistically different among the hosts (Student–Newman–Keuls test, $\alpha = 0.05$).

($F = 5.057$; $df = 4, 39$; $P = 0.0022$). Similarly, the confirmatory assessment, in which the number parasitized host larvae were counted, also revealed a significant of difference in preference of the parasitoid for the different host insects ($F = 5.326$; $df = 4, 345$; $P = 0.000358$). Moreover, *S. frugiperda* and *S. littoralis* recorded the highest number of parasitized larvae, whereas *C. partellus* larvae were least parasitized (Fig. 1).

Comparing the number of female wasps recorded in jars that held the *Spodoptera* spp. and stemborers larvae, within the first 10 min, there were a higher number of *C. icipe* females in jars holding *S. littoralis* (22.2%) followed by *S. frugiperda* (11.1%), with the least parasitoids in the stemborers (Fig. 2). However, the number of parasitoids that sought and/or oviposited on the different host larvae increased over time across host species, after the first 10–50 min of recording. Within that time (10–50 min) and comparing the proportion of parasitoids in the jars holding stemborers, *C. icipe* had high affinity towards *S. calamistis* followed by *C. partellus*; the lowest number was found in *B. fusca* (Fig. 2). Even though the highest number of parasitoids were observed on *Spodoptera* species throughout the experimental period, there was an increase in the number of wasps that sought and/or oviposited in the stemborers, between 20 and 50 min, followed by a general decrease in actively searching and/or ovipositing wasps (between

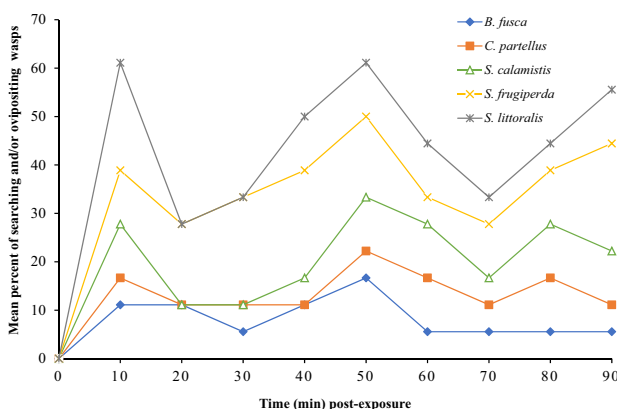


Figure 2. Average proportion of *Cotesia icipe* searching for and/or ovipositing in different host species under multiple-choice test.

60 and 70 min), after which (70–90 min) the activity of the wasps increased again with more wasps recorded in *Spodoptera* spp.

3.2 Host acceptability by *C. icipe*

Under no-choice test scenarios, *C. icipe* accepted all the host larvae for oviposition, albeit with a significant difference in the number of host larvae accepted ($F = 8.252$; $df = 4, 545$; $P = 0.000182$) and the number parasitoid eggs deposited in each host larva ($F = 3.943$; $df = 4, 195$; $P = 0.00428$). *Spodoptera* spp. were the most accepted host insects, whereas *C. partellus* was least accepted (Fig. 3). Comparing the average number of parasitoid eggs deposited in each larva, there were more eggs oviposited in stemborers than the *Spodoptera* spp. (Fig. 3).

3.3 Host physiological suitability for *C. icipe* offspring development

3.3.1 Developmental time of immature stages

Comparative assessment of the developmental duration of *C. icipe* across the tested host species showed a delayed developmental time in stemborers compared with that in *Spodoptera* spp. Even though all the parasitoid eggs hatched within 48 h, the incubation period varied significantly across the host species ($F = 3.1$; $df = 4, 144$; $P = 0.0175$), being shortest in *S. littoralis* (90% hatched within 36 h) and longest in *C. partellus* (30% within 36 h) (Table 1). Similarly, larval developmental duration differed significantly with host species ($F = 124.8$; $df = 4, 20$; $P < 0.001$). On the other hand, time from cocoon formation to wasp eclosion was comparable across host species ($F = 0.357$; $df = 4, 20$; $P = 0.836$). Overall, host species had a significant effect ($F = 150.7$; $df = 4, 20$; $P < 0.001$) on the total developmental time of *C. icipe*, being longest in stemborers and shortest in the *Spodoptera* spp. (Table 1).

3.3.2 Cocoon formation and wasp eclosion

The number of cocoons formed varied significantly with the host species ($F = 27.62$; $df = 4, 20$; $P < 0.001$), being highest in *Spodoptera* spp. and lowest in the stemborers (Table 1). Similarly, the number of wasps eclosed from the host insects was significantly different among the hosts ($F = 52.18$; $df = 4, 20$; $P < 0.001$), whereby a greater number of wasps eclosed from *Spodoptera*

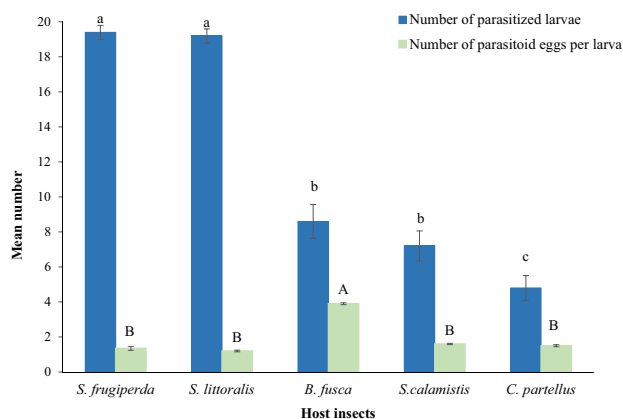


Figure 3. Mean number of parasitized larvae and parasitoid eggs per larva. Means with same lower case letters show that number of parasitized host larvae is not statistically different among the hosts, whereas the same uppercase show that the mean number of parasitoid eggs oviposited in each host larva are not significantly different across the host insects (Student–Newman–Keuls test, $\alpha = 0.05$).

species compared with those that emerged from the stemborers (Table 1).

3.3.3 Encapsulation rate

Assessment of the immunological response of the host larvae to parasitization by *C. icipe* revealed that none of the parasitoid eggs were encapsulated or melanized by any of tested host species, except for *C. partellus* where there was a very low encapsulation rate ($0.05\% \pm 0.05\%$).

3.4 Effect of rearing host on fitness parameters of *C. icipe*

3.4.1 Sex ratio

Cotesia icipe was female biased, and its sex ratio was comparable ($F = 0.49$; $df = 4, 19$; $P = 0.743$) across host species (Table 1).

3.4.2 Body size

Host species had a considerable effect on wasp body size as measured by length and width of the left forewing and the left hind tibia length. The wing length ($F = 39.27$; $df = 3$; $P < 0.001$) and width ($F = 33.42$; $df = 3$; $P < 0.001$), were significantly different across the host species. *Cotesia icipe* wasps that emerged from parasitized *S. littoralis* had the longest wing length and width, whereas those that emerged from *S. calamistis* had the shortest wing length and width (Table 2). Likewise, the hind tibia length of the parasitoid progenies varied with the rearing host ($F = 13.18$; $df = 3$; $P < 0.001$), with those that emerged from *S. frugiperda* having the longest left tibia length, whereas progenies from *S. calamistis* had shortest hind tibia length.

3.4.3 Adult longevity

Longevity of *C. icipe* progenies was affected by host species for both sexes ($F = 13.84$; $df = 2, 33$; $P < 0.001$ and $F = 11.43$; $df = 2, 33$; $P < 0.001$, for male and female respectively); being longest in *S. frugiperda* and shortest in *B. fusca* (Table 1). Comparing the longevity for *C. icipe* reared on the same host species, females survived for longer than the males in *S. frugiperda* ($t_{(22)} = 2.254$; $P = 0.035$); however, the longevity of the males was comparable in both *S. littoralis* ($t_{(22)} = 0.079$; $P = 0.98$) and *B. fusca* ($t_{(22)} = 1.3286$; $P = 0.197$).

4 DISCUSSION AND CONCLUSION

Biological control of insect pests involves choosing an efficient parasitoid. However, the choice of a parasitoid is influenced by several factors, among which is its foraging behaviour.³⁵ In that regard, it is important to assess the foraging behaviour of parasitoids, which include investigation of parasitoid behaviour in location of the host and/or habitat with potential patches of suitable host species, host acceptance for oviposition, preference for different host species, sex allocation and number of offspring,³⁶ among others. Nevertheless, the foraging behaviour of a parasitoid is influenced by the complexity and diversity of the insect community within an ecosystem.³⁷ Thus, our study findings lay the basis for appreciating the foraging behaviour of *C. icipe* in a maize agroecosystem in Africa, as well as the implications of its newfound host association on its potential use in the biocontrol of *S. frugiperda*.

Cotesia icipe preferred *Spodoptera* spp. to stemborers, in terms of searching, probing and oviposition behaviours towards host larvae. The preference for *Spodoptera* spp. in *C. icipe* could be linked to co-evolutionary interactions between this parasitoid and several African species in this genus, including *S. littoralis*,

Table 1. Suitability of different host species for development of *Cotesia icipe* from egg to wasps, and the sex ratio of the parasitoids progenies

Host species	Developmental duration Egg (incubation period in hours)	Larva (in days)	cocoon to adult (in days)	Egg to adult eclosion (in days)	No. of cocoons formed	Total no. of eclosed wasps	Total no. of eclosed male	Total no. of eclosed female	Sex ratio (% female progeny)
<i>Spodoptera frugiperda</i>	39.6 ± 1.74a	7.8 ± 0.18a	4.2 ± 0.18a	12.0 ± 0.00a	19.4 ± 0.37a	18 ± 0.29a	6.40a	11.6 ± 0.76a	64.28 ± 3.44a
<i>Spodoptera littoralis</i>	37.2 ± 1.14b	8.0 ± 0.28a	4.4 ± 0.49a	12.4 ± 0.22a	19.4 ± 0.37a	19 ± 0.29a	6.60a	12.4 ± 0.48a	65.23 ± 2.03a
<i>Busseola fusca</i>	38.4 ± 1.52c	14.8 ± 0.44c	4.4 ± 0.22a	19.2 ± 0.52c	14.2 ± 0.91b	13.6 ± 0.64b	5.20ab	8.4 ± 0.48b	61.76 ± 4.55a
<i>Sesamia calamistis</i>	38.4 ± 1.51c	10.8 ± 0.52b	4.4 ± 0.22a	15.2 ± 0.44b	13.8 ± 0.81b	12.8 ± 0.69b	5.20ab	7.6 ± 0.48b	59.38 ± 3.71a
<i>Chilo partellus</i>	44.4 ± 1.74d	19.0 ± 0.40d	4.6 ± 0.22a	23.6 ± 0.36d	11 ± 0.67c	9.2 ± 0.55c	3.80b	5.4 ± 0.48c	58.70 ± 4.50a

Note: Means in each column followed by the same letter are not significantly different (Student–Newman–Keuls test, $\alpha = 0.05$).

Table 2. Effect of rearing host on fitness parameters of *Cotesia icipe*

Host insect	Sex ratio	Body size (mm)			Longevity	
		Wing length	Wing width	Hind tibia length	Female	Male
<i>Spodoptera frugiperda</i>	64.28 ± 3.44a	2.41 ± 0.02b	0.74 ± 0.01 c	0.88 ± 0.01 a	25.83 ± 0.04a	18.83 ± 0.06a
<i>Spodoptera littoralis</i>	65.23 ± 2.03a	2.51 ± 0.03a	0.93 ± 0.01 a	0.78 ± 0.01 b	20.16 ± 0.06a	19.92 ± 0.05a
<i>Busseola fusca</i>	61.76 ± 4.55a	2.31 ± 0.03c	0.83 ± 0.01 b	0.72 ± 0.01 c	11.26 ± 0.05b	8.83 ± 0.05b
<i>Sesamia calamistis</i>	59.38 ± 3.71a	2.26 ± 0.05c	0.82 ± 0.02 b	0.71 ± 0.02 c	*	*
<i>Chilo partellus</i>	58.70 ± 4.50a	*	*	*	*	*

Note: Means in each column followed by the same letter are not significantly different (Student–Newman–Keuls test, $\alpha = 0.05$).

*Insufficient number of females to study adult body size and longevity using the same sample size ($n = 15$) as the three host insects (*S. frugiperda*, *S. littoralis*, and *B. fusca*).

S. exigua (Hübner) and *S. exempta* (Walker) (both Lepidoptera: Noctuidae). It has been argued that parasitoids exhibit 'strong congruent choices' for their co-evolved hosts.³⁸ For example, Mohamed *et al.*³⁹ demonstrated that the Asian parasitoid, *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae) preferred and performed best on its co-evolved host *Bactrocera invadens* (*B. dorsalis*) (Diptera: Tephritidae) compared with the African *Ceratitis* species. Another aspect that might explain host differential preference by *C. icipe* could be related to olfactory and visual cues from host larvae, a phenomena that has been documented in other host–parasitoid systems.^{35,40,41} For instance, kairomones from *S. frugiperda* frass and other host-produced materials were found to stimulate host searching and attack behaviour in the congeneric parasitoid, *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) and consequently strengthen its preference for the host.⁴² Although not tested in this study, kairomones produced by *Spodoptera* spp. could be more attractive in terms of quality and quantity compared with those of the stemborers, which could therefore influence the preference of *C. icipe* for *Spodoptera* spp. Similarly, Obonyo *et al.*⁴³ projected that the differences in tactile and contact-chemoreception stimuli by *Cotesia sesamiae* and *C. flavipes* (both Hymenoptera: Braconidae) could have influenced the parasitoid's oviposition choice for *B. fusca*, *C. partellus* and *Eldana saccharina* Walker (Lepidoptera: Pyralidae).

The differential preference by *C. icipe* for different host species, which translated to a varying degree of acceptability of the tested hosts to the parasitoid, in terms of the number of parasitized host larvae could be linked to optimization theory. Based on optimization theory, insect mothers are expected to oviposit more on resource-rich hosts for development of their progenies and to attain the highest exclusive fitness.⁴⁴ Furthermore, the differential preference by the parasitoid could be influenced by two factors: (i) the *per capita* quality of *Spodoptera* spp. resources may have been higher than in stemborers; and (ii) *Spodoptera* spp. may have excess resources for *C. icipe* progenies to utilize.⁴⁴ Indeed, our result is in line with previous findings for other parasitoid species,^{39,45} which supports optimization theory. For instance, *C. sesamiae* and *C. flavipes* also variably accepted stemborers, *B. fusca*, *C. partellus* and *E. saccharina*,⁴³ a decision which could have been guided by internal cues of the host larvae, as perceived by the ovipositing female wasp.⁴⁶

Cotesia icipe is a solitary endoparasitoid²⁵; however, self-superparasitism is often recorded in first- and second-instar larvae of its parasitized host,²⁸ but only one parasitoid larva survives in the host larva. In this study, *C. icipe* oviposited a higher number of eggs per larva in stemborers compared with *Spodoptera* spp. This could be linked to the advantages of superparasitism in

ensuring successful parasitism. White and Andow⁴⁷ reported that superparasitism is associated with, among other things, host immune response avoidance. For example, *Microplitis rufiventris* Kokujev (Hymenoptera: Braconidae) laid only one egg on early instars (high-quality hosts) of *S. littoralis*, and superparasitized late instars (low-quality) of the same host.⁴⁸ Thus, in this study, *C. icipe* could have recognized *Spodoptera* spp. as more suitable hosts with higher chances of progeny survival relative to stemborers, thus the higher number of eggs laid in stemborers to counteract the host defence. This is substantiated by the earlier finding that *C. icipe* laid more eggs in the less suitable third-instar larvae of *S. frugiperda* compared with the first-instar larvae.²⁸

Host suitability mirrored host acceptability, whereby *Spodoptera* spp. were found to be more suitable for development of *C. icipe* than stemborers for the number of cocoons formed and wasps enclosed, and overall developmental time, with the former parameter being shorter in *Spodoptera* spp., whereas the latter two parameters (number of wasps enclosed and overall developmental time) were higher on these host species. Similar findings on differences in the suitability of *Cotesia* spp. parasitoids have been recorded in *Cotesia plutellae* Cameron (Hymenoptera: Braconidae) on 15 different lepidopteran hosts,⁴⁹ as well as in *C. sesamiae* on *B. fusca*, *Sesamia cretica* Lederer and *Poconoma serrata* Tams & Bowden (both Lepidoptera: Noctuidae).⁵⁰ Notably, differential host physiological suitability for an endoparasitoid is a function of host regulation factors. The factors such as the host's internal environmental conditions, including the sufficiency and suitability of the nutritional source, ultimately shape the outcome of possible completion of parasitoid development.³⁵ For instance, it has been argued that the physiology of the host larvae could result in the: (i) death of the immature stages of a parasitoid, (ii) differences in developmental time, (iii) fewer cocoons formed, (iv) male-biased sex ratios or (v) shorter longevity of the progenies (Rezaei *et al.*,³⁵ and reference therein). In that regard, *Spodoptera* spp. could have provided the right combination of environmental conditions, such as sufficiency and suitability of the nutritional source, for the development of the parasitoid progenies compared with the stemborers. Indeed, *C. icipe* has been reported to have a longer developmental time when it parasitized third and fourth instars of *S. frugiperda*.²⁸

Generally, the success of any parasitoid as an augmentative or inundative biocontrol agent is determined by several fitness traits such as sex ratio,⁵¹ where female-biased sex ratio is a desired trait in biocontrol.⁵² In this study, we demonstrated that *C. icipe* had a female-biased ratio in all the host species, a finding similar to previous studies in which *C. icipe* was found to be female biased

irrespective of the host stage attacked on both *S. frugiperda*²⁸ and *S. littoralis*.²⁵ Other related species that exhibit a female-biased sex ratio irrespective of the host species they were offered include *C. plutellae*⁵³ and *C. flavipes*.⁵⁴ The fact that *C. icipe* is female biased in all the tested hosts, makes it a very promising candidate for biological control of these pests, especially *S. frugiperda* and *S. littoralis*.

Other fitness traits such as body size and adult longevity are also key determinants of a parasitoid's behavioural ecology.⁵⁵ Our study revealed that *C. icipe* offspring emerging from *Spodoptera* spp. were of better quality in terms of both body size and adult longevity than those emerging from the stemborers. It is well established that progeny body size and adult longevity are affected by the quality of the host at the time of the oviposition, including the nutritional status (Harvey *et al.*,⁴⁴ and reference therein). Based on this, it can be argued that *Spodoptera* spp. offered a superior quality host compared with stemborers, thereby yielding more fit parasitoid progenies. Parasitoid body size is also positively correlated with egg production, longevity, competition for access to mates and dispersal.⁵⁶ Using the same analogy, the superior body size of *C. icipe* progenies from *Spodoptera* spp. could explain the longer life span of wasps eclosed from these hosts compared with their counterparts eclosed from *B. fusca*. A similar effect of rearing host on these fitness traits has been reported by Rakawa *et al.*⁵⁷ and Woltering *et al.*⁵⁸ for other parasitoid species.

Overall, our findings demonstrate that *C. icipe* is able to form new association with the recent invader, *S. frugiperda*, with outstanding performance in terms of host preference, acceptability and suitability compared with the stemborers. These findings have different implications on the use of this parasitoid in augmentative or inundative field release for suppression of these pests. First, the finding that *C. icipe* can successfully develop in other sympatric pest species of maize (stemborers), regardless of its parasitism rates on stemborers, may have negative consequences on the efficiency of the parasitoid against the target pest (in this case, *S. frugiperda*) in the field. Therefore, caution is needed when undertaking augmentative releases in areas dominated by stemborers by possibly increasing the number of wasps released in the field; although recent studies by Sokame *et al.*⁵⁹ and Hailu *et al.*⁶⁰ revealed that *S. frugiperda* is displacing stemborers in maize fields. Second, successful development of the parasitoid on both *Spodoptera* spp. and stemborers could contribute to an increase in *C. icipe* population over several generations of *S. frugiperda* in the field. Despite being a generalist parasitoid, this may be a good strategy for the existence and establishment of *C. icipe* on other hosts whenever the population of *S. frugiperda* in the field is low. Moreover, the existence of *S. littoralis* on other plants such as *Amaranthus* spp. in the same maize field may not reduce the efficiency of *C. icipe* in suppressing populations of *S. frugiperda* in the same field, but confer an advantage of continuous existence of the parasitoid over several generations. In conclusion, *C. icipe* demonstrated a strong potential to control *S. frugiperda* in maize because of its high affinity for parasitization and developmental success in this host; and despite its non-specific parasitization, the presence of other hosts may not prevent its maximum control of *S. frugiperda*.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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