International Journal of Tropical Insect Science (2021) 41:157–168
https://doi.org/10.1007/s42690-020-00188-7

ORIGINAL RESEARCH ARTICLE

# Oviposition behavior of *Telenomus busseolae, Telenomus isis* and *Trichogramma bournieri* on eggs of east African cereal stemborers

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Received: 28 November 2019 / Accepted: 12 June 2020 / Published online: 30 July 2020

## Abstract

The oviposition behavior of the scelionids *Telenomus busseolae, Telenomus isis* and the trichogrammatid *Trichogramma bournieri* was studied on eggs of lepidopteran cereal stemborers, which included the noctuid *Busseola fusca*, *Sesamia calamistis, Sesamia nonagrioides,* the crambid *Chilo partellus*, and the pyralid *Eldana saccharina*. Unlike *Tr. bournieri*, *Telenomus* spp. did not attack eggs of *C. partellus* and *E. saccharina*. Five distinct behavioral steps were observed, which included foraging, drumming with the antennae on the eggs, ovipositor insertion, egg marking, and walking and resting. Foraging, walking and resting were observed less frequently than the other behaviors. There was a clear hierarchy of behavioral steps leading to successful parasitism, which culminated in marking of eggs. Self-superparasitism (i.e., oviposition in an egg previously parasitized by the same female) was between 2.7–5.9% indicating that the three parasitoids were able to discern eggs that were already parasitized. Earlier studies on the bionomics and host finding ability together with the present findings on the oviposition behavior of the different parasitoids cannot explain differences in parasitism rates by the parasitoids in the field. It is suggested that the plant species and alternative hosts occurring in crop and natural habitats may play an important role in the population dynamics of the parasitoids and affect their importance in controlling key pests of maize.

**Keywords** Egg parasitoids · Cereal stemborers · Superparasitism · Oviposition behavior

## Introduction

Cereals are the most important crops grown in Africa (Kfir 1999). In East and Southern Africa (ESA), the noctuid *Busseola fusca* (Fuller) and the crambid *Chilo partellus* (Swinhoe) are the economically most important stemborers while *Sesamia calamistis* (Hampson), *Sesamia nonagrioides* (Lefebvre), and *Eldana saccharina* (Walker) are minor species co-occurring in the same agroecological zones (Songa et al. 2001; Zhou et al. 2001; Le Rü et al. 2006; Calatayud et al. 2014). Yield losses estimates are in the range of 10 to 50% (van Rensburg et al. 1988; De Groote 2002; Chabi-Olaye et al. 2005; Gounou et al. 2009; Robert et al. 2014).

Biological control is a significant factor of pest suppression especially in small holder farming systems in Africa and egg parasitoids are an important source of mortality because the pest is killed before damaging the crop (Temerak 1981; Schulthess et al. 1997). In the humid lowland tropics of western Africa, the scelionid egg parasitoids *Telenomus busseolae* Gahan and *Telenomus isis* Polaszek are important mortality factors of eggs of noctuid cereal stemborers such as *S. calamistis* and *B. fusca* (Sétamou and Schulthess 1995; Schulthess et al. 2001; Ndemah et al. 2002). In contrast to *T. busseolae*, *T. isis* has never been reported from East and Southern Africa (ESA) (Polaszeck 1998; Moyal 1998; Ndemah et al. 2001; Chabi-Olaye et al. 2006). Thus, the parasitoid was introduced into the containment facilities of the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya, in 2003, for release against

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*B. fusca*, which is the major pest of cereals in the mid-altitude and highlands of the region (Kfir et al. 2002).

In eastern Africa, the most common egg parasitoid is *T. busseolae* and less important the trichogrammatid, *Trichogramma bournieri* Pintureau and Babault. While the former is oligophagous attacking eggs of noctuids only, the latter is polyphagous parasitizing eggs of noctuids, crambids and pyralids (Bournier 1983; Bonhof 2000; Haile et al. 2000; Bruce et al. 2006, 2009a). In a survey carried out in the mid-altitudes and highlands in Kenya by Bruce et al. (2009b), parasitism by *T. busseolae* were 10–60% and mostly above 20%, while for *Tr. bournieri* they were 1–6% only.

Egg parasitoids of stemborers hunt for egg batches at very low densities in cultivated and natural habitats (Sétamou and Schulthess 1995; Ndemah et al. 2000; Gounou and Schulthess 2004; Chabi-Olaye et al. 2005; Bruce et al. 2009b). Still parasitism can reach regional means of 95% (Schulthess et al. 2001) indicating an excellent host finding ability of the parasitoids. Bruce et al. (2009c) showed that the two *Telenomus* spp. and the trichogrammatid *Tr. bournieri* responded to calling virgin *S. calamistis*, *S. nonagrioides* and *B. fusca* but there was no difference in the attractiveness between the three borer species. Thus, the parasitoids not only have to compete with conspecific females but also with females of other parasitoid species, which might affect the establishment and parasitization rates of *T. isis* in ESA.

The roles of the different semiochemicals involved in host finding of egg parasitoids of cereals stemborers are complex. Besides pheromones, kairomones present on the plant (Chabi-Olaye et al. 2001a) or the egg surface (Nordlund et al. 1987; Bin et al. 1993; Conti et al. 2003), scales left by the female moth (Lewis et al. 1971, 1972; Colazza and Rosi 2001) or host recognition kairomone associated with the female accessory gland secretion, which is used as adhesive for the egg mass (Bin et al. 1993; DeSantis et al. 2008), may not only contribute to host finding but also influence the acceptability of the host eggs.

This study was carried out to elucidate and compare the ovipositional behavior of *T. busseolae*, *T. isis* and *Tr. bournieri* on eggs of *S. calamistis*, *S. nonagrioides*, *B. fusca*, *C. partellus* and *E. saccharina* in order to provide first information on the ability of *T. isis* to parasitize East African stemborer species and populations, and of the chances of its establishment in the new areas.

## Material and methods

### Rearing of hosts and parasitoids

The insect species used were reared in the laboratories at ICIPE (Lat: −1.2219; Long: 36.8967). The stemborers included *C. partellus* from the coastal region of Kenya, *B. fusca* from Kitale, Western Kenya, *S. calamistis* from Machakos, Eastern Kenya, *S. nonagrioides* from Eastern and Western Kenya, and *E. saccharina* from Mbita, Western Kenya. Apart from *S. nonagrioides* collected from *Typha domingensis* in Makindu and Kisii, all stemborers were collected from maize plants. They were reared on diets developed by Ochieng et al. (1985) and Onyango and Ochieng-Odero (1994). Parasitoid colonies were established on *B. fusca* eggs following the protocol developed by Chabi-Olaye et al. (1997). *Telenomus isis* was obtained from the laboratories of the International Institute of Tropical Agriculture (IITA), Republic of Benin, while *T. busseolae* and *Tr. bournieri* were collected from *B. fusca* eggs at, Eldoret and Mbita, respectively, in Kenya. The two *Telenomus* species were kept in separate rooms in order to prevent contamination of the colonies. All insects were reared at 25 ± 1 °C and 65 ± 5% RH.

### Oviposition behavior

This study was carried out with the aim of establishing the ovipositional events that lead to successful parasitization of hosts by *T. isis, T. busseolae* and *Tr. bournieri* using no-choice bioassays. Twelve to 18-h old egg batches from *B. fusca, S. calamistis*. *S. nonagrioides, C. partellus* and *E. saccharina* containing on an average 45 eggs, were exposed to a 1-day-old mated, naive female of *T. isis, T. busseolae* and *Tr. bournieri*. Each egg in an egg batch was numbered. The behavior of each female was observed under a binocular microscope from the first contact with the host eggs onward. All instances of oviposition, single attack and self-superparasitism (i.e., oviposition in an egg previously parasitized by the same female) were recorded. Observations either ended when the female had parasitized all eggs or when she left the batch without returning. Thereafter, the parasitized batches were kept at 25 ± 1 °C and 65 ± 5% RH until emergence of the parasitoids. The percentage parasitism was determined.

The behavior of a female parasitoid was described in terms of her body posture and movement whilst in contact with a host egg. The behavioral steps are mutually exclusive events described as a combination of orientation and movement of different body parts especially those bearing sensory structures (i.e., antennae, tarsi and ovipositor). In the present study, five behavioral steps were exhibited by the female parasitoids: (1) Foraging ("fora"): a female walked in the arena (Petri dish) while palpitating the antennae until she mounted the egg mass placed on a maize leaf. In contrast to egg masses of hosts, female wasps never stopped and kept moving when offered egg masses of non-hosts; (2) Palpitation ("palp"): the female wasp began examining several eggs by antennal palpitation and then settled on one of the eggs; (3) Oviposition ("ovip"): the female inserted its ovipositor into the host egg; (4)

Marking ("mark"): after withdrawing the ovipositor, the parasitoid scraped the egg surface with the tip of its ovipositor with a characteristic circular movement, thereby marking the egg; (5) Walking and resting("walk and rest"): the female left the egg mass, walked around it in the Petri dish and then rested next to the egg mass. The duration of each behavioral step was recorded. Palpitation, oviposition and marking were observed for each egg in a mass while foraging, resting and walking were monitored only once per female and for the entire egg batch.

The experiment was replicated 15 times with different females for each stemborer host and parasitoid species. Each female was used only once. All borer species were tested with each parasitoid species irrespective of their suitability.

### Egg volume

This study was carried out to determine if there was any relationship between volume or size of the host egg and the number of progeny of *Tr. bournieri*, which, in contrast to *Telenomus* spp., is a gregarious species. The volume of an egg was estimated by using the ellipsoidal formula by Preston (1974):

$V = (\pi/6)LB^2$[| 1]where L is the length and B the maximum diameter of an egg. The measurements were taken with an ocular micrometer under a Lieca M3Z microscope. The calibration of the microscope was done according to the method developed by Billah et al. (2005).

### Statistical analysis

Data on the duration of each event, parasitism (percentage of eggs parasitized once), super parasitism (percentage of eggs parasitized more than once), and the percentage of emergence of parasitoids were subjected to analysis of variance (ANOVA) using the general linear (GLM) model in SAS Institute (1997). In case of significant F values, means were compared using the Student-Newman-Keuls test. The significance level was set at $P \leq 0.05$. The linear regressions were run to assess if there was any relationship between volume or size of the host egg and the number of progenies of *Tr. Bournieri.*

For every parasitoid species, the behavior of 15 females encountering the host egg batches were analyzed using Proc Catmod (SAS Institute 1997) in a procedure similar to that of Parr et al. (1996) and Hora and Roessingh (1999). The analysis of their behavior was conducted on the total number of transitions between all possible pairs of behavioral steps and the data was pooled for all females using transitional frequencies of all transitions between pairs of behavioral patterns.

The probability of each transition given the preceding behavior was also calculated. To identify the transitions that were a significant part of a sequence of behavioral steps, standardized residuals of the observed transitions were calculated, when compared to a model that did not include the assumption of dependence of following and preceding behavioral steps. Significant positive transitions, i.e. those for which positive standardized residuals were obtained, greater than the calculated threshold were used to construct kinetograms of the host recognition, acceptance and suitability behavior.

## Results

### Foraging and oviposition behavior

Female parasitoids displayed the same five behavioral steps when offered suitable hosts (Table 1). First, a parasitoid walked in the Petri dish without showing any particular behavior. At times it walked on unsuitable host eggs but without palpitating or trying to oviposit. Typically for each parasitoid species, the female started by examining several eggs by antennal palpitation. The palpitation ceased when the parasitoid positioned itself with the posterior legs in contact with the egg and inserted its ovipositor. The parasitoid examined each host egg several times before starting to oviposit. The beginning of oviposition was characterized by sudden repeated contraction of the cervix, which caused the female's head to move in pumping motion. After the pumping activity, the female remained motionless until oviposition was completed. Upon withdrawing the ovipositor, the female backed from the host egg twisting its abdomen from side to side so that the ovipositor made a sinuous track in a figure-eight pattern on the accessible portion of the egg surface. Female wasps showed two types of ovipositor-insertion posture. In most cases, they inserted their ovipositors into the lateral side of the host egg and rarely into the upper part. In a few cases (less than 2%), *Tr. bournieri* licked the egg surface with the mandibles. This could be indicated as host feeding.

On suitable hosts, all kinetograms indicated a clear sequential transition in the behavioral steps that were exhibited by all parasitoid species studied irrespective of parasitism rates obtained on suitable hosts (Figs. 1, 2 and 3; Table 1). They most likely oviposited after palpitation (highest probability values recorded between "Palp" and "Ovip") and thereafter they most likely marked the eggs after oviposition. The other behavioral steps (i.e., "Fora" and "Rest") occurred occasionally. The lowest probability values were recorded between "Fora" and "Palp", and between "Mark" and "Rest". Thus, according to the kinetograms the female parasitoids exhibited most likely "Palp", "Ovip" and "Mark". However, although the transitional probabilities for palpitation after foraging were very low, foraging behavior occurred for most of the wasps observed; the percentage of occurrence mostly around 90%.

There were significant differences in the duration of each behavioral event among host and parasitoids species

**Table 1.** Duration (seconds ± S.E.) of oviposition events by *T. busseolae*, *T. isis* and *Tr. bournieri* per egg mass by *B. fusca*, *S. nonagrioides, S. calamistis, C. partellus* and *E. saccharina*

| Parameters | Parasitoids | Stemborer hosts | | | | | Statistical test | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *B. fusca* | *S. nonagrioides* | *S. calamistis* | *C. partellus* | *E. saccharina* | F | DF | P |
| Foraging time (sec) | *T. busseolae* | 1734.8 ± 41.52bB | 742.0 ± 16.06aA | 1604.7 ± 30.88bB | - | - | 3.70 | 2, 42 | 0.0332 |
| | *T. isis* | 600.6 ± 12.16a | 500.4 ± 82.06a | 650.2 ± 71.16a | - | - | 1.11 | 2, 38 | 0.3399 |
| | *Tr. bournieri* | 836.3 ± 12.51aA | 2332.3 ± 21.67bB | 1368.7 ± 24.18abB | 940.4 ± 99.63A | 892.13 ± 15.99A | 5.48 | 4, 70 | 0.0007 |
| | F | 2.53 | 18.96 | 3.29 | | | | | |
| | DF | 2,44 | 2,41 | 2,42 | | | | | |
| | P | 0.0332 | <.0001 | 0.0471 | | | | | |
| Palpitation time (sec) | *T. busseolae* | 1048.0 ± 86.34 | 1672.0 ± 25.49b | 1360.6 ± 15.03b | - | - | 1.10 | 2, 42 | 0.3427 |
| | *T. isis* | 956.8 ± 11.07 | 748.4 ± 93.03a | 813.0 ± 10.95a | - | - | 0.36 | 2, 42 | 0.6998 |
| | *Tr. bournieri* | 971.8 ± 82.64B | 750.1 ± 54.91aAB | 666.4 ± 81.71aA | 1206.6 ± 12.01B | 924.6 ± 13.41AB | 3.54 | 4, 70 | 0.0109 |
| | F | 0.65 | 6.75 | 5.77 | | | | | |
| | DF | 2,42 | 2,42 | 2,42 | | | | | |
| | P | 0.5256 | 0.0029 | 0.0061 | | | | | |
| Oviposition time (sec) | *T. busseolae* | 3561.7 ± 30.54aA | 6015.4 ± 54.15aB | 3799.6 ± 31.17aA | - | - | 5.71 | 2,39 | 0.0069 |
| | *T. isis* | 4184.6 ± 43.08a | 6664.5 ± 83.38b | 4708.2 ± 53.73a | - | - | 0.63 | 2,41 | 0.5404 |
| | *Tr. bournieri* | 5963.0 ± 74.22bAB | 9723.5 ± 68.04cB | 7213.8 ± 43.50bAB | 2894.9 ± 18.33A | 6504.6 ± 92.05AB | 1.03 | 4,69 | 0.0398 |
| | F | 79.44 | 201.44 | 212.89 | | | | | |
| | DF | 2,40 | 2,41 | 2,42 | | | | | |
| | P | <.0001 | <.0001 | <.0001 | | | | | |
| Marking time (sec) | *T. busseolae* | 276.8 ± 22.13b | 464.6 ± 64.61c | 313.8 ± 29.98b | - | - | 3.21 | 2, 42 | 0.0506 |
| | *T. isis* | 348.6 ± 43.57b | 280.5 ± 36.68b | 336.2 ± 38.74b | - | - | 0.30 | 2, 42 | 0.7460 |
| | *Tr. bournieri* | 133.6 ± 21.55aA | 98.4 ± 2.97aA | 265.6 ± 19.67aB | 260.6 ± 32.48B | 238.8 ± 61.08AB | 5.09 | 4, 70 | 0.0012 |
| | F | 7.42 | 30.29 | 14.05 | | | | | |
| | DF | 2,42 | 2.42 | 2,42 | | | | | |
| | P | 0.0017 | <.0001 | <.0001 | | | | | |
| Resting time (sec) | *T. busseolae* | 1179.0 ± 14.89 | 2034.2 ± 44.24b | 1986.8 ± 71.63 | - | - | 0.45 | 2, 17 | 0.6455 |
| | *T. isis* | 1079.2 ± 39.19 | 751.0 ± 16.83a | 982.2 ± 17.96 | - | - | 0.52 | 2, 12 | 0.6085 |
| | *Tr. bournieri* | 919.4 ± 20.41 | 1157.4 ± 25.50ab | 1150.7 ± 93.38 | 839.7 ± 12.39 | 886.5 ± 15.45 | 0.78 | 4, 19 | 0.5516 |
| | F | 0.54 | 4.19 | 1.28 | | | | | |
| | DF | 2,13 | 2,20 | 2,11 | | | | | |
| | P | 0.5979 | 0.0321 | 0.3173 | | | | | |

Means within column followed by the same lower-case letter(s) and means within rows followed by the same capital case letter(s) were not significantly different (SNK test; P < 0.05).

(Table 1). Foraging time on *B. fusca* egg masses was longer for *T. busseolae* than for *T. isis* and *Tr. bournieri*. Using *S. nonagrioides* as host foraging time was shorter for the two *Telenomus* species than *Tr. bournieri*. For *Tr. bournieri*, foraging time did not vary significantly with host except on *S. nonagrioides*, where it was more than double, and in most cases, it was not significantly different from those of the *Telenomus* spp. (Table 1). Palpitation time did not vary significantly for the two scelionids irrespective of host, but on *Sesamia* spp. it was shorter for *T. isis* than *T. busseolae*. For *Tr. bournieri*, it was significantly shorter on *S. calamistis* than *C. partellus* but it did not vary significantly among the other hosts. On *Sesamia* spp., it was significantly longer than that of *T. busseolae*.

For both scelionids, oviposition duration did not vary with host species but with *S. nonagrioides* it was shorter for *T. isis* than *T. busseolae*. For *bournieri*, it did not vary significantly with most host species, though it tended to be shortest on *C. partellus*, and on *Sesamia* spp. longer than those of *Telenomus* spp. Differences in marking time between hosts and *Telenomus* species were mostly not significant except for *S. nonagrioides* on which it was shorter for *T. isis* than *T. busseolae*. On hosts they had in common, marking time of *Tr. bournieri* was shorter than that of *Telenomus* spp. Resting and walking periods did not vary with host and parasitoid species except for *T. isis* for which it was shorter than *T. busseolae* with *S. nonagrioides* as host (Table 1).

## Parasitism, self-superparasitism

Parasitism of either *Telenoms* sp. did not vary within or between host species (Table 2). For *Tr. bournieri*, however, it was higher on *S. nonagrioides* and *C. partellus* than other hosts. Self-superparasitism was low ranging between 2.7 and 7.9%. For *T. busseolae* it was lowest on *B. fusca*, while for *T. isis* it did not vary with host. For *Tr. bourneiri* it was lowest on *B. fusca* and similar on the other hosts. Differences between the trichogrammatid and the scelionids were with one exception not significant. Parasitism before self-superparasitism (PSS) started varied between 44.1 and 79.6 (Table 2). For any of the host, it did not vary between parasitoid species, and it varied significantly with host species for *T. busseolae* and *Tr. bournieri* (Table 2). For *T. isis* PSS was higher with *S. nonagrioides* than the other hosts, while for *Tr. bournieri*, it was highest with *S. nonagrioides* and lowest with *B. fusca* as host.

For *T. busseolae*, progeny number per host did not vary with host species while for *T. isis,* it was higher with *S. calamistis* than *S. nonagrioides* as host (Table 2). Within host species, progeny numbers did not vary among *Telenomus* spp. But it was always higher and more than one for *Tr. bournieri* than *Telenomus* spp. *Tr. bournieri* had the highest number of progeny per host with *S. nonagrioides* and lowest with *C. partellus* where progeny number was less than one (Table 2).

The egg volumes varied significantly with host species; it was largest for noctuids followed by *E. saccharina* and *C. partellus* ($F = 582.10$, $df = 4499$, $P < 0.0001$). The egg volume in $\mu m^3$ (± S.E) was 341,974.3 ± 697.1 for *B. fusca*, 351,494.1 ± 641.5 for *S. nonagrioides,* 336,781.5 ± 552.5 for *S. calamistis*, 107,086.2 ± 263.8 for *C. partellus* and 302,944.1 ± 782.0 for *E. saccharina*. For *Tr. bournieri*, the number of progeny per host (x) was significantly positively correlated with host volume ($y = 192{,}182 + 56{,}947x$, $r^2 = 0.87$, $P < 0.0001$). Similarly, there was a positive relationship between oviposition period and *Tr. bournieri* progeny production (x) ($y = 4553.1 + 45.1x$, $r^2 = 0.73$, $P < 0.0001$).

## Discussion

The behaviors observed for the three parasitoids are similar to those of many species in the Scelionidae and Trichogrammatidae families (Hokyo and Kiritani 1966; Rabb and Bradley 1970; Strand and Vinson 1983a; Higuchi and Suzuki 1996; Wiedemann et al. 2003). On unsuitable hosts, none of the behavioral steps leading to oviposition took place. There were significant differences in foraging and palpitation time between host and parasitoid species, but they appeared not to influence parasitism.

The three parasitoids drummed the host eggs with the antennae indicating that they were the most important structures involved in host location and identification. The antennae contain many receptors utilized in host detection (Slifer 1969; Miller 1972; Norton and Vinson 1974). Thus, rejections or acceptance of the host may be due to tactile stimuli or in response to contact chemicals (kairomones) elicited by the host (Vinson 1976). Furthermore, the three parasitoids mounted the host during foraging, thus, the tarsi could also be involved in host recognition (Strand and Vinson 1983a).

Oviposition time was considerably longer for *Tr. bournieri* than for the *Telenomus* species. It did not vary between *T. isis* and *T. busseolae*, except on *S. calamistis*, where it took considerably longer for *T. busseolae*, which was the reverse of the results by Agboka et al. (2002) in West Africa. Behavioral variation within a species may be due to strain differences in both parasitoids and hosts. For example, Wajnberg and Colazza (1998) comparing different iso-female lines of *Trichogramma brassicae* Bezdenko (Hymenoptera; Trichogrammatidae) found a significant genetic variability in the surface they were able to prospect per unit of time. Furthermore, Colazza and Rosi (2001) showed differences in the searching behavior of two strains of *T. busseolae*, one from Turkey and the other one from West Africa. In addition, phylogenetic studies in Africa by Sézolin et al. (2006), Assefa et al. (2006), and Ong'amo et al. (2008) identified several distinct populations of *B. fusca, E. saccharina* and *S. calamistis*, which varied in their host plant range and climatic requirements. Quality and especially size of the host could also affect the oviposition behavior of the parasitoids.

In Hymenoptera, the ovipositor may be involved in host detection but it is more important in host acceptance (Vinson 1977; Larocca et al. 2007). Agboka (1998) and Strand and Vinson (1983b) showed that *T. busseolae*, *T. isis* and *T. heliothis* lay eggs 30–40 s after insertion of the ovipositor, which was accompanied by head pumping. Thus, egg laying occurs only immediately before ovipositor withdrawal as also reported for *Telenomus remus* Nixon (Hymenoptera: Scelionidae) (Gerling and Schwartz 1974) and *T. heliothidis* (Strand and Vinson 1983a). This indicates that the parasitoid is first assessing the suitability of the host using the ovipositor. Sensory structures on the ovipositor of parasitoids are implicated in detection of host quality in general (Fisher 1971; Greany et al. 1977).

Host marking is common in many hymenopterous parasitoids. In the scelionid *Trissolcus mitsukurii* Ashmead, *Telenomus nakagawai* Watanabe (Hokyo and Kiritani 1966), and *Telenomus shingis* Ashmead (Rabb and Bradley 1970), the marking behavior was not exhibited when a female failed to oviposit. This could be due to the host already being parasitized (Darrouzet et al. 2007). Furthermore, Strand and Vinson (1983a) reported that marking immediately followed egg oviposition in *Telenomus heliothis* Ashmead (Hymenoptera: Scelionidae). Therefore, marking is a good indicator of successful oviposition in these egg parasitoids.

Noctuid stemborers are relatively weak flyers, which lay 10–20 egg batches in a random to regular manner within a relatively small area of less than half an acre (Sétamou and Schulthess 1995; Schulthess et al. 2001; Chabi-Olaye et al. 2005; Bruce et al. 2009b). In addition, *Telenomus* spp. are

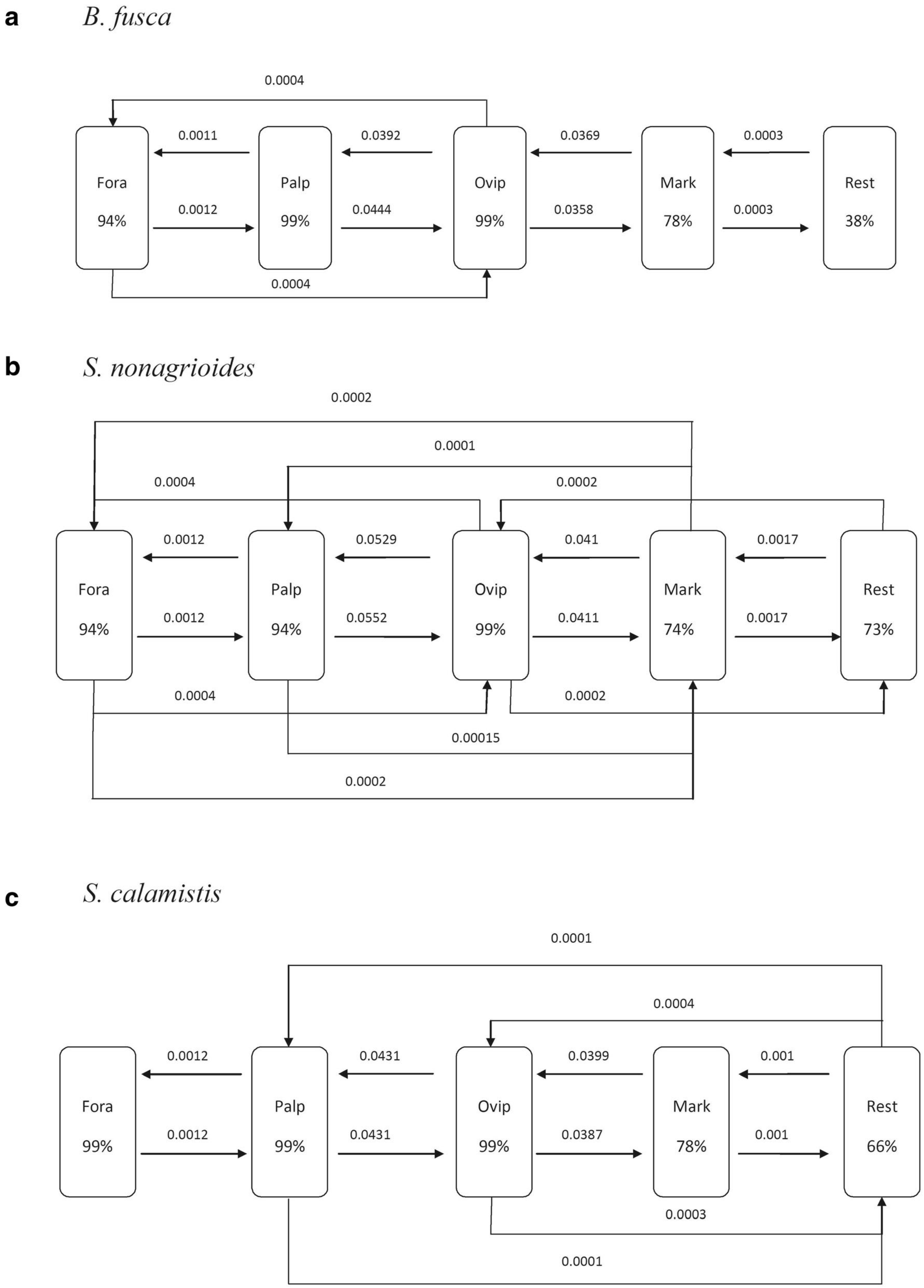


**Fig. 1** Behavioural steps exhibited by naive gravid females of *T. busseolae* in contact with *B. fusca* (**a**), *S. nonagrioides* (**b**) and *S. calamistis* (**c**) eggs. Decimal numbers with the arrows represent the probability of each significant transition given the preceding behaviour. For each experiment, 15 female parasitoids were observed. The percentage of occurrence of each behavioural step is given below its category definition

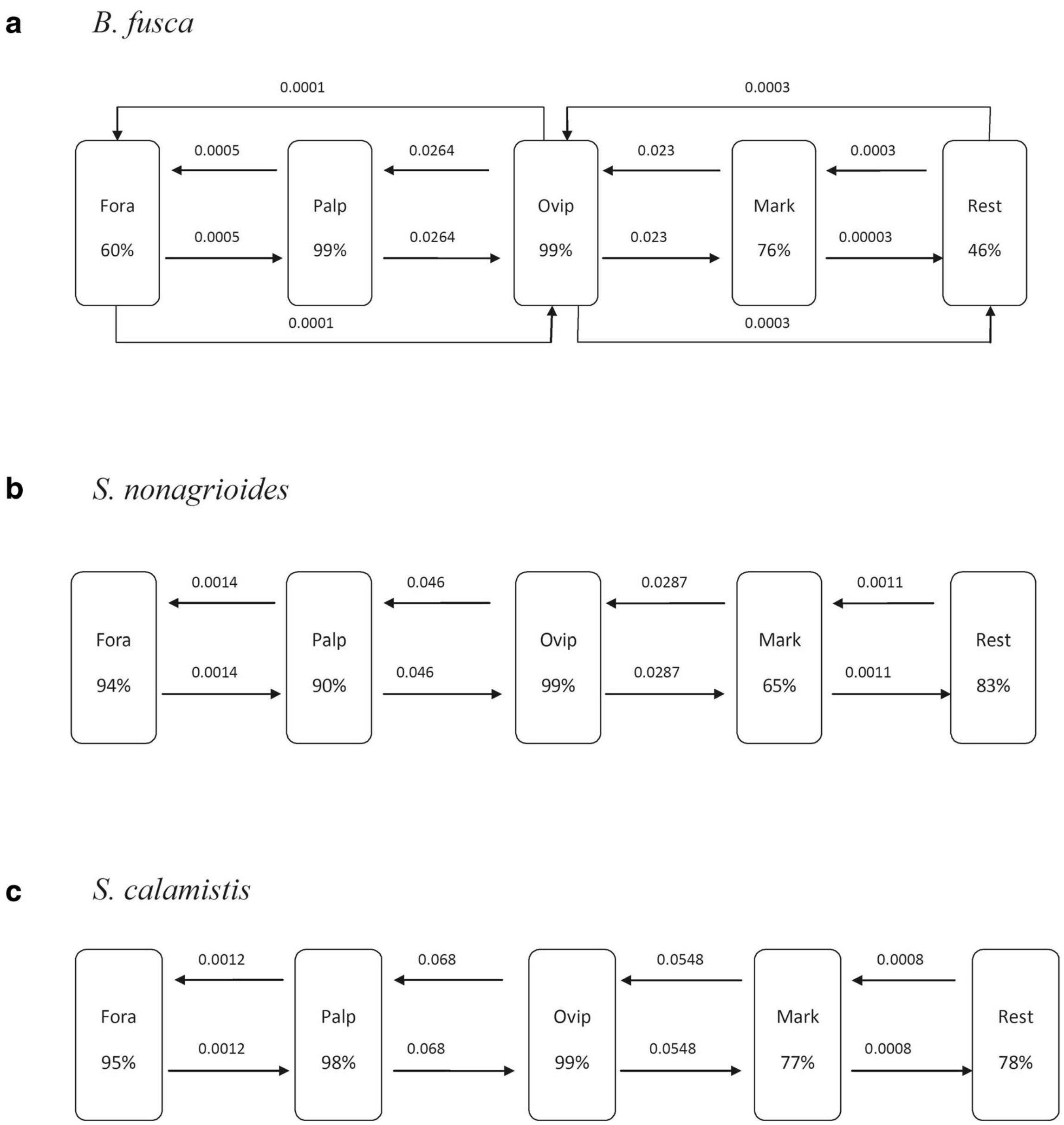
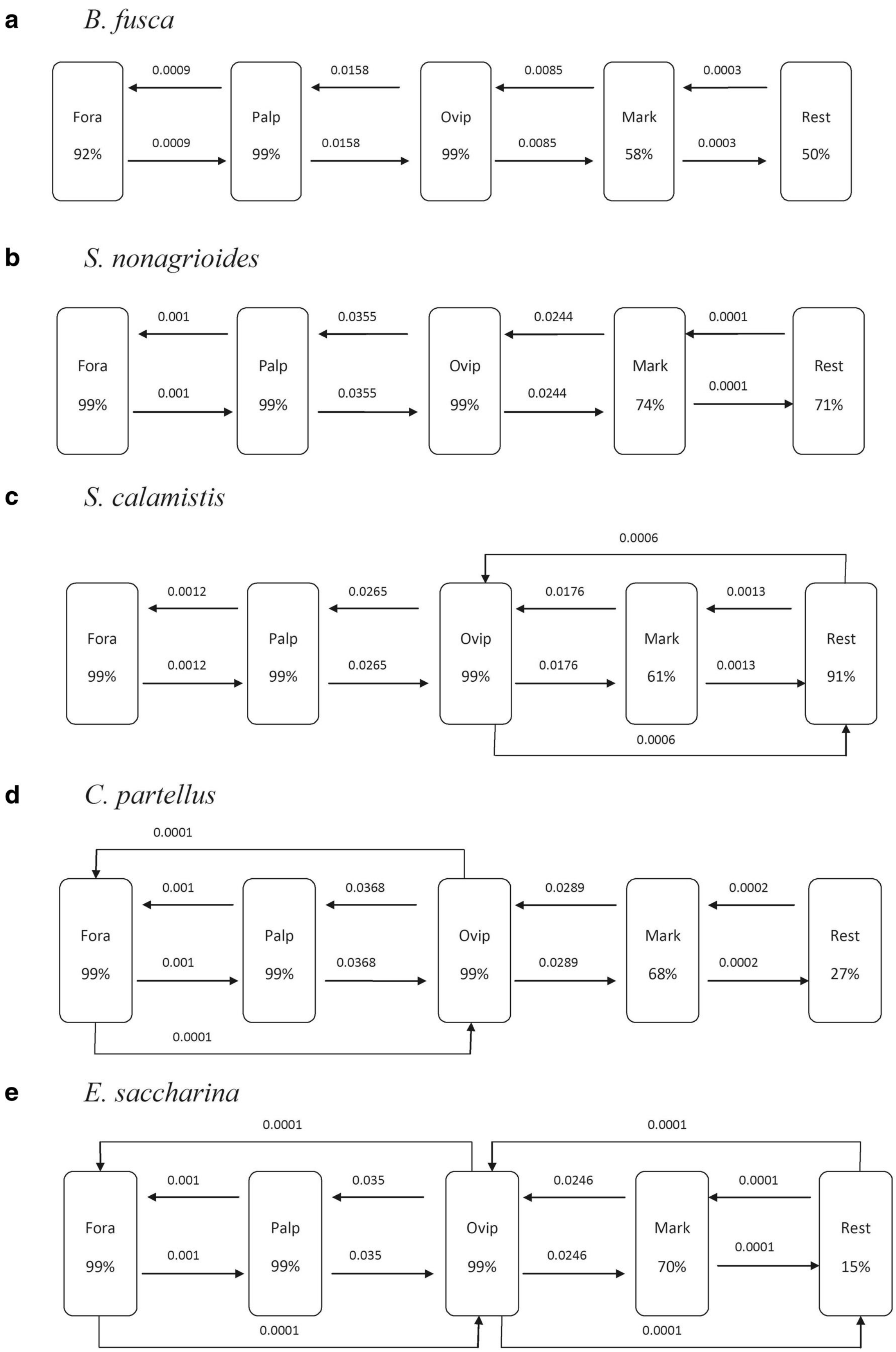


**Fig. 2** Behavioural steps exhibited by naive gravid females of *T. isis* in contact with *B. fusca* (**a**), *S. nonagrioides* (**b**) and *S. calamistis* (**c**) eggs. Decimal numbers with the arrows represent the probability of each significant transition given the preceding behaviour. For each experiment, 15 female wasps were observed. The percentage of occurrence of each behavioural step is given below its category definition

attracted by pheromones of the virgin female moth and probably scales left at the oviposition event (Chabi-Olaye et al. 2001a; Fiaboé et al. 2003; Bruce et al. 2009c). Hence, the chances of an individual parasitoid from the same or different cluster, or a female of a different species discovering the same egg batch are relatively high, especially for "quasi-gregarious" species (Weber et al. 1996), which exploit eggs occurring in discrete clusters and for which mating occurs between siblings. In this situation, self intraspecific host discrimination is an important characteristic of a parasitoid. The present findings indicate that all three parasitoids exhibited self-intraspecific host discrimination and therefore avoided ovipositing in already parasitized eggs. This corroborates results by Agboka et al. (2002), who showed that the two *Telenomus* species were capable of intra- and interspecific host discrimination, which could be related to the marking behavior of the parasitoid. Because super parasitism reduces offspring quality and survival, most parasitoids developed a mechanism that enables them to distinguish already parasitized hosts (Rabb and Bradley 1970; van Lenteren 1976; Bosqué and Rabinovich 1979; Strand and Vinson 1983a; van Alphen and Visser 1990; Agboka et al. 2002). However, long periods of host deprivation lead to egg resorption and female fecundity decreases gradually, but faster in *T. isis* than in *T. busseolae,* and faster in *Tr. bournieri* than *Telenomus* spp. (Chabi-Olaye et al. 1997, 2001a; Bruce et al. 2006,


a
B. fusca
Fora 92%
Palp 99%
Ovip 99%
Mark 58%
Rest 50%
0.0009
0.0158
0.0085
0.0003
0.0009
0.0158
0.0085
0.0003
b
S. nonagrioides
Fora 99%
Palp 99%
Ovip 99%
Mark 74%
Rest 71%
0.001
0.0355
0.0244
0.0001
0.001
0.0355
0.0244
0.0001
c
S. calamistis
0.0006
Fora 99%
Palp 99%
Ovip 99%
Mark 61%
Rest 91%
0.0012
0.0265
0.0176
0.0013
0.0012
0.0265
0.0176
0.0013
0.0006
d
C. partellus
0.0001
Fora 99%
Palp 99%
Ovip 99%
Mark 68%
Rest 27%
0.001
0.0368
0.0289
0.0002
0.001
0.0368
0.0289
0.0002
0.0001
e
E. saccharina
0.0001
0.0001
Fora 99%
Palp 99%
Ovip 99%
Mark 70%
Rest 15%
0.001
0.035
0.0246
0.0001
0.001
0.035
0.0246
0.0001
0.0001
0.0001

◀ **Fig. 3** Behavioural steps exhibited by naive gravid females of *T. bournieri* in contact with *B. fusca* (**a**), *S. nonagrioides* (**b**), *S. calamistis* (**c**), *C.partellus* (**d**) and *E. saccharina* (**e**) eggs. Decimal numbers with the arrows represent the probability of each significant transition given the preceeding behaviour. For each experiment, 15 female wasps were observed. The percentage of occurrence of each behavioural step is given below its category definition

2009b). Thus, a female may choose to super- or multiparasitism rather than to continue searching for a suitable host. However, as indicated by the present finding and by Agboka et al. (2002), super- and multiparasitism are rare among the two *Telenomus* spp. and very likely will not affect establishment of *T. isis* in eastern Africa.

In some cases, female wasps withdrew their ovipositor without exhibiting the marking behavior. In these cases, the wasps left the egg mass but then always returned to it. Similarly, Hokyo and Kiritani (1966) reported that females of *T. mitsukurii* rest on or beside the host egg masses early in the oviposition period, but they did not explain the significance of this behavior. Takasu and Hirose (1993) observed that females of *Ooencyrtus nezarae* Ishii (Hymenoptera: Encyrtidae) often rested during the host acceptance behavior. They hypothesized that the wasp takes a rest to digest the host fluid after host feeding. However, host feeding was only observed for *Tr. bournieri* and in less than 5% of the parasitized eggs in a batch.

For *Tr. bournieri*, which in contrast to *Telenomus* spp. lays more than one egg per host, the number of progeny per host was significantly positively related with the egg volume of the host. This corroborates results by Nurindah Cribb and Gordh (1999), who found that *Trichogramma* spp. lay more eggs in larger than smaller hosts. Thus, larger hosts may be of superior quality (Singh et al. 1998).

While in western and central Africa peak parasitism by *Telenomus* spp. are commonly above 80% and positively affect maize yields, parasitism by *T. busseolae* in Kenya is usually below 40% and that of *Tr. bournieri* below 5% (Sétamou and Schulthess 1995; Schulthess et al. 2001; Ndemah et al. 2003; Bruce et al. 2009c). Other factors, such as the plant habitat and alternative hosts not tested in the present study as well as host specificity could play a role. Chabi-Olaye et al. (2001a) showed that *T. isis* was more attracted by *S. calamistis* eggs when they were offered on maize and sorghum than on millet leaf sheath, or egg batches offered without leaf sheaths. Also, in the laboratory, *T. isis* accepted and parasitized eggs of 12 noctuid borer species (i.e., 7 *Sesamia*, 2 *Busseola*, 2 *Manga* and 1 *Sciomesa*) (Bruce et al. 2009a) found in cultivated and wild habitats (Le Rü et al. 2006).

**Table 2.** Percentage parasitism, self-superparasitism and progeny (± S.E.) of *T. busseolae, T. isis, Tr. bournieri* using eggs by *B. fusca*, *S. nonagrioides*, *S. calamistis*, *C. partellus* and *E. saccharina*

| Parameters | Parasitoids | Stemborer hosts | | | | | Statistical test | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *B. fusca* | *S. nonagrioides* | *S. calamistis* | *C. partellus* | *E. saccharina* | F | DF | P |
| Parasitism (%) | *T. busseolae* | 81.4 ± 4.5 | 75.6 ± 8.8 | 66.7 ± 9.1 | - | - | 0.80 | 2, 42 | 0.4548 |
| | *T. isis* | 68.9 ± 6.8 | 74.2 ± 6.5 | 74.8 ± 6.1 | - | - | 0.30 | 2, 42 | 0.7397 |
| | *Tr. bournieri* | 78.8 ± 6.0B | 82.5 ± 7.9A | 69.6 ± 8.5B | 90.9 ± 3.3A | 71.3 ± 7.0B | 2.33 | 4, 70 | 0.0442 |
| | F | 1.39 | 0.62 | 0.13 | | | | | |
| | DF | 2,44 | 2,44 | 2,44 | | | | | |
| | P | 0.2597 | 0.5426 | 0.8766 | | | | | |
| Self-superparasitism (SSP) (%) | *T. busseolae* | 5.0 ± 0.89bA | 7.9 ± 0.39bB | 5.6 ± 0.83AB | - | - | 3.69 | 2, 42 | 0.0334 |
| | *T. isis* | 5.9 ± 0.05b | 6.9 ± 0.54ab | 4.9 ± 0.91 | - | - | 1.73 | 2, 42 | 0.1898 |
| | *Tr. bournieri* | 2.7 ± 0.04aA | 5.6 ± 0.86aB | 6.6 ± 0.66B | 6.0 ± 0.58B | 7.5 ± 0.63B | 6.81 | 4, 68 | 0.0001 |
| | F | 2.91 | 3.64 | 1.12 | | | | | |
| | DF | 2,43 | 2,44 | 2,43 | | | | | |
| | P | 0.0456 | 0.0349 | 0.3368 | | | | | |
| Parasitism before SSP started (%) | *T. busseolae* | 54.1 ± 9.2 | 69.2 ± 3.5 | 63.5 ± 7.4 | - | - | 1.44 | 2, 42 | 0.2486 |
| | *T. isis* | 54.4 ± 8.7B | 68.1 ± 3.9A | 56.8 ± 8.3B | - | - | 5.47 | 2, 42 | 0.0078 |
| | *Tr. bournieri* | 51.0 ± 1.0B | 79.8 ± 3.1A | 69.3 ± 6.2AB | 73.2 ± 4.1AB | 63.5 ± 5.6AB | 3.08 | 4, 69 | 0.0215 |
| | F | 0.24 | 1.74 | 0.72 | | | | | |
| | DF | 2,44 | 2,44 | 2,43 | | | | | |
| | P | 0.7888 | 0.1874 | 0.4937 | | | | | |
| Progeny per parasitized host | *T. busseolae* | 0.74 ± 0.04b | 0.81 ± 0.03b | 0.77 ± 0.04b | - | - | 0.85 | 2, 42 | 0.4342 |
| | *T. isis* | 0.81 ± 0.05bAB | 0.72 ± 0.05bB | 0.90 ± 0.03bA | - | - | 3.43 | 2, 42 | 0.0416 |
| | *Tr. bournieri* | 1.87 ± 0.17aB | 2.41 ± 0.27aA | 1.56 ± 0.17aBC | 0.95 ± 0.05D | 1.19 ± 0.13C | 8.88 | 4, 70 | <.0001 |
| | F | 31.79 | 34.11 | 15.50 | | | | | |
| | DF | 2,44 | 2,44 | 2,44 | | | | | |
| | P | <.0001 | <.0001 | <.0001 | | | | | |

Means within column followed by the same lower-case letter(s) and means within rows followed by the same capital case letter(s) were not significantly different (SNK test; P < 0.05).

They could serve as alternative hosts and thereby influence the population dynamics of a parasitoid species.

From the studies carried out so far it can be concluded that competition with *T. busseolae*, the most common egg parasitoid of *B. fusca* in eastern Africa, and the gregarious *Tr. bournieri* will not affect the establishment of *T. isis* in the region.

**Acknowledgements** The authors wish to thank George Okumu, Mercy Mwaloh and Evelyn Olanga for their technical support during the experiments. This work was supported by the Directorate General for International Cooperation, The Netherlands and a student fellowship to the senior author by the German Academic Exchange Service (DAAD).

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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