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ORIGINAL ARTICLE

Superparasitism and its effects on the fitness of the larval parasitoid, *Coccygidium luteum* (Hymenoptera: Braconidae)

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Abstract. The tendency of parasitoid wasps to oviposit in a previously parasitised host (superparasitism) has long been considered detrimental to their fitness, until recent evidence showed that it may be an adaptive strategy. The solitary koinobiont parasitoid, *Coccygidium luteum*, was observed to superparasitise the fall armyworm, *Spodoptera frugiperda*, under laboratory conditions. This study was conducted to elucidate the oviposition choice between unparasitised and previously parasitised hosts by *C. luteum* and to determine the effect of superparasitism on progeny development and adult fitness, using fall armyworm larvae as hosts. In a choice assay, previously parasitised and unparasitised hosts were simultaneously exposed to *C. luteum* for oviposition. Oviposition duration and preference were observed and the influence of superparasitism on the development of immature parasitoids and adult fitness were investigated by exposing host larvae to single, double and triple parasitism at 1 h intervals. *Coccygidium luteum* readily attacked both unparasitised and previously parasitised hosts without discrimination. However, the time spent ovipositing on the unparasitised host was significantly longer than that on a previously parasitised host. Superparasitism did not significantly affect progeny development and the fitness of adult *C. luteum*. Offspring development time and size of adult parasitoids were similar in superparasitised hosts compared to hosts that were parasitised once. We conclude that superparasitism in *C. luteum* will have no effect on its mass rearing for the biological control of *S. frugiperda*.

INTRODUCTION

Parasitoids are a group of insects that are parasitic only in their immature stages and free-living as adults. They usually live and survive on the tissues of immature stages of a particular group of insect species. These immature stages of the host remain their sole source of food, unlike predators which consume a variety of prey. Host quality is a major determinant of the physical and reproductive fitness of adult parasitoids, as parasitoid larvae are restricted to the limited food resources in their hosts (Farahani et al., 2016). Host quality is influenced by many factors, including age, size (Gao et al., 2016) and whether the host was previously parasitised (Van Alphen & Visser, 1990; Plantegenest et al., 2004). Unparasitised hosts are expected to guarantee greater chances of survival and fitness for the parasitoid due to the availability of adequate food resources for the developing parasitoid larvae compared to previously parasitised hosts, which are considered to be of poor nutritional quality (Charnov & Skinner, 1985). However, when good quality or unparasitised hosts are scarce, female parasitoids may be forced to accept and oviposit in a poor quality host, such as a previously parasitised host. Previously parasitised hosts are thought to be of low quality because the nutritional resources are insufficient to support parasitoid development and fitness, as multiple parasitoid larvae compete for limited host contents.

Parasitoid competition for hosts occurs when adult females search a patch for a host to oviposit on, or when two or more larvae depend on the same host contents for development. Parasitoids do not remove the host from the patch after oviposition and are likely to encounter a previously parasitised host. Such previously parasitised hosts may be accepted for further oviposition, a situation known as superparasitism. Superparasitism occurs when a female oviposits in a host previously parasitised by itself (self-superparasitism) or by other female(s) of the same species

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(conspecific superparasitism). It is a common occurrence in parasitoids and has been observed in several species, both in the field and in the laboratory. In gregarious parasitoid species, a single host can support the development of several larvae. In solitary species, however, only one larva will develop into an adult, regardless of the number of eggs laid. Therefore, superparasitism in solitary parasitoids is considered to be detrimental to their fitness because it leads to a waste of eggs, energy and time of the ovipositing wasp (Van Alphen & Visser, 1990; Gandon et al., 2006). Furthermore, there is ample evidence that superparasitism increases developmental time (Harvey et al., 1993; Gu et al., 2003), decreases the survival of the superparasitised host and ultimately the immature parasitoid (Gu et al., 2003), and reduces the size of the progeny (Duval et al., 2018).

Despite the long-held view that superparasitism is maladaptive, available evidence suggests that it may also be an adaptive strategy (Van Alphen & Visser, 1990). Indeed, it has been proposed that self-superparasitism in solitary parasitoids could be beneficial if it increases the probability of producing offspring from a host, the survival of offspring against conspecific competition, or the encapsulation of the first egg by the host (Van Alphen & Visser, 1990). Furthermore, self-superparasitism can be beneficial in the sense that it improves the sex ratio (White & Andow, 2008). On the other hand, conspecific superparasitism may be beneficial when high quality hosts are scarce and the second larva is more likely to survive the competition and develop into an adult (Bakker et al., 1985). The fitness costs of superparasitism are highly variable. For example, in *Dendrocerus carpenter* (Curfis) (Megaspilidae), conspecific superparasitism resulted in a female-biased sex ratio, supporting the notion that superparasitism may be beneficial (Mackauer & Chow, 2016). In another study, delayed developmental time of *Ooencyrtus pityocampae* (Mercet) (Encyrtidae) was observed in a superparasitised host, *Samia cynthia ricini* (Jones) (Lepidoptera: Saturniidae) (Tunca et al., 2016).

It has been shown that some hymenopteran parasitoid species avoid superparasitism by recognising parasitised hosts through chemical cues or host markers deposited in or on the host during oviposition (Stelinski et al., 2007). These substances provide information to the individual and other females about the status of the host. The aim of host marking is to allow females to recognise and avoid already parasitised hosts or previously visited patches, thereby avoiding super- and multiple-parasitism (Van Alphen & Visser, 1990; Ruschioni et al., 2015). However, because marking substances are the same within species, conspecifics can recognise parasitised hosts or a patch used by other females. Host marking is therefore considered an adaptive strategy to deter self and conspecific superparasitism and to prevent competition between progenies, thereby increasing their chances of survival (Stelinski et al., 2007). While not every parasitoid species has evolved the ability to discriminate between hosts, even in the order Hymenoptera, where this tendency is widespread, some species with this ability are still able to exhibit superparasitism. Some species can avoid self-superparasitism by exploiting a patch alone (Van Alphen, 1988). Other species such as *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae) can discriminate between self and conspecific parasitised hosts (Hubbard et al., 1987). Van Alphen (1988) observed a positive correlation between the number of females exploiting a patch and superparasitism, suggesting that the higher the number of species exploiting a patch, the higher the likelihood and incidence of superparasitism.

The phenomenon of superparasitism can occur in several parasitoid species of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), in Africa. These include the solitary koinobiont endoparasitic wasp *Coccygidium luteum* (Brullé) (Hymenoptera: Braconidae), a parasitoid of lepidopteran species. *Coccygidium luteum* has been reported in several African countries (Agboyi et al., 2020; Caniço et al., 2020; Abang et al., 2021; Otim et al., 2021) attacking *S. frugiperda*, which invaded the continent in 2016 (Goergen et al., 2016; Cock et al., 2017) and has since become an endemic pest. *Coccygidium luteum* is a potential candidate for augmentative biological control of *S. frugiperda* due to its ability to attack early instar larvae (1st to 3rd instar) of the host, significantly reducing the feeding rate of parasitised larvae by over 80% (Agboyi et al., 2019). During laboratory rearing, we observed that *C. luteum* revisits and parasitises previously parasitised hosts multiple times. As *C. luteum* is considered a promising larval parasitoid of *S. frugiperda* to be promoted in an augmentative biological control programme, knowledge of the effect of superparasitism on progeny development and fitness is important in designing protocols for its mass rearing. Therefore, we investigated (i) the choice between parasitised and unparasitised hosts by *C. luteum*, (ii) the duration of oviposition in parasitised and unparasitised hosts by *C. luteum*, and (iii) the effect of superparasitism on the development time and fitness of the parasitoid.

MATERIAL AND METHODS

Insect culture

Coccygidium luteum and *Spodoptera frugiperda* were reared in the laboratory at a temperature of 29°C ± 2°C, 70% ± 5% relative humidity and a photoperiod of 12L : 12D. The initial colonies of *S. frugiperda* and *C. luteum* were obtained from *S. frugiperda* larvae collected from maize fields in Somanya, a town in the Eastern region of Ghana, in 2021. The larvae were fed on fresh young maize leaves until they formed cocoons or pupae. *C. luteum* and *S. frugiperda* that emerged from the cocoons and pupae, respectively, were used to establish the initial culture for the parasitoids and the host. Both insects were reared in the laboratory for over two years, resulting in more than 22 generations by periodically revitalising the parasitoid and host colonies by collecting and introducing individuals of the same species from the field. The *S. frugiperda* culture was maintained on fresh young maize leaves. The leaves were replaced with fresh plant materials every two days, while the adult moth and parasitoid wasp were fed on droplets of honey smeared on the inner walls of the oviposition cages. Water was supplied to the insects through cotton wool soaked in water and placed at the bottom of the cages.

After eclosion, adult *C. luteum* males and females were allowed to mate for 48 h in 50 ml plastic vials with droplets of honey on the inner walls and a ball of cotton wool soaked in water placed at the bottom of the vials. After 48 h of mating, the females were transferred to PET bottles (diameter 2.87 cm; volume 250 ml) with aerated lids, which were used as oviposition cages. *S. frugiperda* larvae were introduced individually into the cages as oviposition substrates for *C. luteum*. The parasitoid wasps were observed for oviposition and the duration of oviposition was recorded. All *S. frugiperda* larvae used in the experiment were second instar larvae (4–5 days old).

Choice test between parasitized and unparasitized larvae

To determine the choice of *C. luteum* between parasitised and unparasitised hosts, three experiments were conducted using naïve females (no oviposition experience before exposure to *S. frugiperda* larvae) and oviposition-experienced females. 'Experienced' refers to females that had oviposited at least once before being used in the experiment. In the first experiment, we investigated the choice by a naïve female between an unparasitised host and a host previously parasitised by another wasp. The second experiment examined the choice of a *C. luteum* female between larvae previously parasitised by the same female and unparasitised larvae. In the third experiment, we examined the choice of an experienced female between an unparasitised host and a host previously parasitised by another female. Host larvae that had been parasitised only once were obtained by exposing second instar larvae to mated parasitoids and allowing them to oviposit in the larvae. Parasitised larvae were immediately removed with a fine camel hair brush and placed in another container. In each test, parasitised and unparasitised hosts were simultaneously exposed to a female and observed for oviposition choice. The first larva visited and parasitised was recorded as preferred. Each of the three experiments was replicated 14 times.

Ovipositor insertion time

Spodoptera frugiperda larvae were exposed to *C. luteum* females for oviposition in oviposition cages as described previously. *Coccygidium luteum* females were observed for oviposition. The total time between insertion of the ovipositor for oviposition and its withdrawal from the host larvae was recorded using a digital timer. Any oviposition attempt lasting less than 2 s was considered unsuccessful and not recorded. To ensure consistency and minimise error, all observations were made and recorded by the same observer.

Influence of superparasitism on progeny development time, cocoon weight and parasitoid size

To determine the effect of superparasitism on the development of *C. luteum* progeny, we tested and compared hosts that had been parasitised once, twice and three times. To ensure that each host was parasitised only once, second-instar larvae were exposed to *C. luteum* females for a single oviposition event in oviposition cages as described previously. Parasitised larvae were immediately removed with a fine camel hair brush and placed in 80 ml sauce cups with aerated lids and labelled accordingly. To obtain superparasitised hosts, *S. frugiperda* larvae that had previously been parasitised once were subsequently exposed to a second group of conspecific female wasps for an additional oviposition (resulting in two eggs per host) and then to a third group for a final round of parasitism (three eggs per host). The interval between each round of parasitism and the next was one hour. The parasitised larvae were kept individually in sauce cups containing tissue paper and fresh young maize leaves. From the eighth day after oviposition, parasitized larvae were monitored three times a day for parasitoid larval egression and cocoon formation. Eclosion of adult wasps was monitored three times daily to ensure accurate recording of developmental time. To determine the effect of superparasitism on adult parasitoid fitness, hind tibia and forewing lengths were measured using a Leica digital microscope (application suite 3.4.0 and camera version 2.0.4.0 with ×8 magnification). Both hind tibiae were measured and the mean was calculated for each individual. The weight of the parasitoid cocoon was measured using a COBOS precision electronic microscope (ATY224) e.1mg; d = 0.1mg.

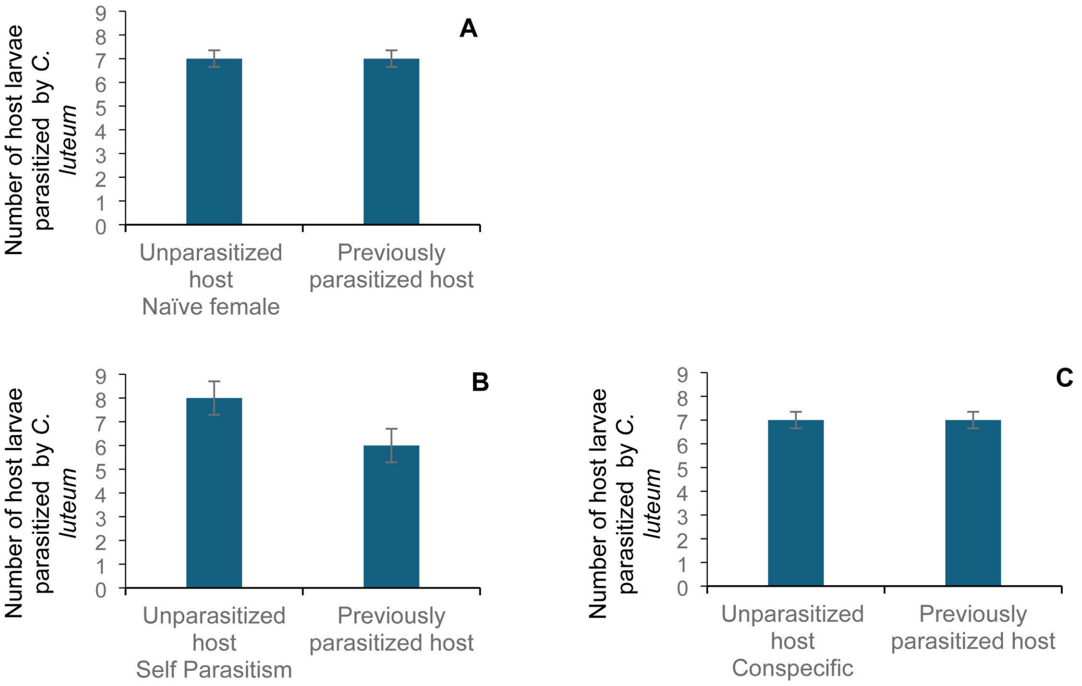

Fig. 1. Oviposition choice by *Coccygidium luteum*. A – choice by naïve females between unparasitised larvae and larvae previously parasitised by another female; B – choice by experienced females between unparasitised larvae and self-parasitised larvae; C – choice by experienced females between unparasitised larvae and larvae previously parasitised by other females.

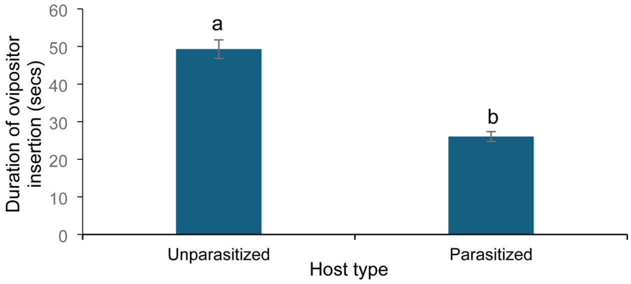

Fig. 2. Mean time that *Coccygidium luteum* ovipositor remained inserted in previously parasitised or unparasitised hosts. Error bars represent standard errors. Different letters above error bars indicate significant difference.

Data analysis

All data were subjected to the Shapiro-Wilk W normality test. Developmental time, cocoon weight and fitness data were analysed using one-way analysis of variance (ANOVA). A Pearson's square test (χ^2) was performed to determine whether there was a significant difference in the selection of parasitised and unparasitised larvae by naïve and experienced (self and conspecific) female wasps. Ovipositor insertion duration was analysed using an equal variance group t-test. All analyses were performed using STATA 17.0 Standard Edition.

RESULTS

Oviposition choice by *C. luteum* between parasitized and unparasitized hosts

Both naïve and experienced *Coccygidium luteum* females readily attacked previously parasitised host larvae, despite the presence of unparasitised host larvae (Fig. 1). No significant difference in preference for parasitised or unparasitised hosts was observed, regardless of whether the female had previous oviposition experience or not [χ^2 (1, n = 14) = 0.9, P = 0.909]. The tendency of female *C. luteum* to parasitise previously parasitised larvae was not influenced by whether the larvae were parasitised by itself or by a conspecific female.

Ovipositor insertion time

The duration of ovipositor insertion in unparasitised hosts was significantly longer than in previously parasitised hosts (P = 0.019). The mean ovipositor insertion time for previously parasitised hosts was 28.25 ± 4.3 s and for unparasitised hosts was 48.23 ± 7.9 s (Fig. 2).

Effect of superparasitism on parasitoid larval developmental time

The number of ovipositions of *C. luteum* in a host had no significant effect on the developmental time of parasitoid larvae. The mean developmental duration of parasitoid larvae was similar in both single and multiple parasitism studies (P = 0.073) (Fig. 3A). Similarly, single or multiple parasitism did not affect the mean developmental time from cocoon formation to adult emergence (P = 0.127) (Fig. 3B). The time from cocoon formation to adult emergence was similar in all three treatments.

Effect of superparasitism on parasitoid fitness

Double or multiple parasitism had no effect on parasitoid fitness when the length of the hind tibia and forewings of the offspring were compared with single parasitism (Fig. 4A and B). Hind tibia lengths were similar in all three treatments (P = 0.518) (Fig. 4A). Similarly, forewing size was similar regardless of parasitism number (P = 0.999) (Fig. 4B). These results suggest that superparasitism had no effect on parasitoid size or fitness.

Effect of superparasitism on cocoon weight

There was no significant effect of superparasitism on cocoon weight. Cocoon weight in single parasitised hosts was not significantly different from double and triple parasitised hosts (Fig. 5). Similarly, cocoon weight in doubly parasitised hosts was not significantly different from that of triple parasitised hosts (P = 0.187).

DISCUSSION

Superparasitism in solitary parasitoid wasps has long been considered a wasteful practice detrimental to parasitoid fitness (Van Lenteren, 1981; Waage, 1986). Host discrimination is considered an adaptive strategy in some parasitoid species to avoid superparasitism (van Baaren et al., 1995). In our study, *Coccygidium luteum* females, whether naïve or experienced, showed no ability to discriminate between parasitised and unparasitised hosts. Host acceptance was similar between naïve and experienced *C.*

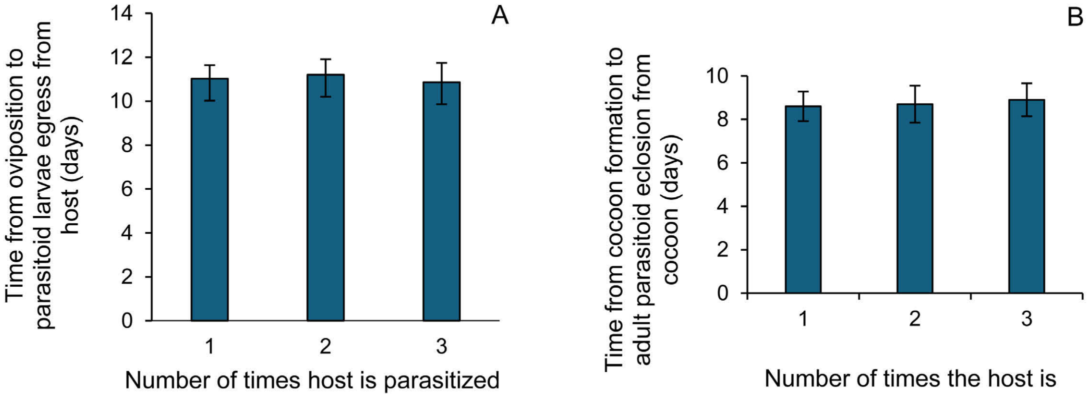

Fig. 3. Mean (± SE) developmental time (in days) of *Coccygidium luteum* from oviposition to parasitoid larval emergence from the fall armyworm host (A) and adult parasitoid eclosion (B).

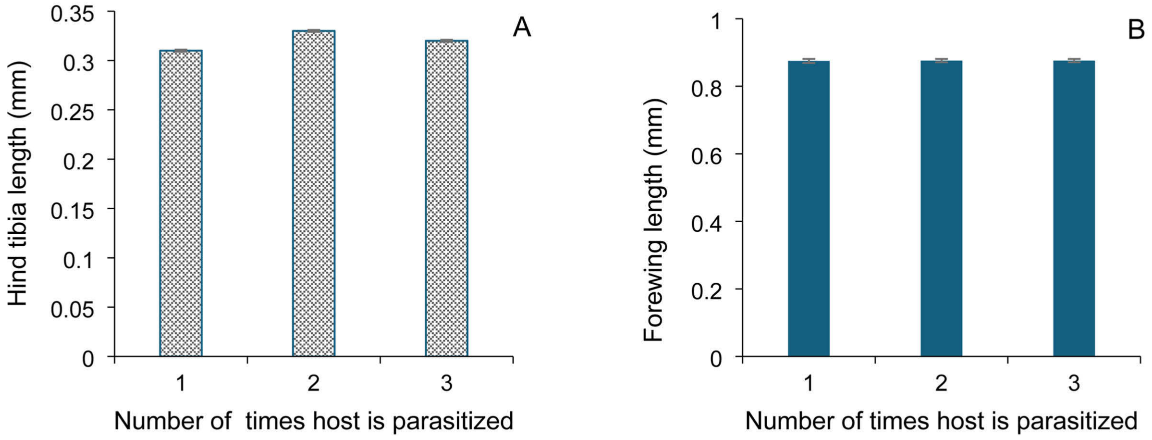

Fig. 4. Mean adult size (mm) ±SE of *Coccygidium luteum* measured based on lengths of hind tibia (A) and forewing (B).

luteum. Naïve *C. luteum* readily accepted both parasitised and unparasitised hosts. Host discrimination is thought to be an acquired trait and may therefore be absent in parasitoids without oviposition experience (Bakker et al., 1972; van Lenteren, 1976; van Baaren & Boivin, 1988). Second, when host availability is limited, naïve parasitoids may be forced to accept and oviposit in the first host they encounter, regardless of its quality. This behaviour may be due to physiological and physical constraints such as longevity, time and egg limitation, as rejection of available hosts may result in the death of such an individual without progeny. Experienced *C. luteum* females were expected to discriminate parasitised hosts, but this was not observed. Similar to the results of Gu et al. (2003), experienced wasps readily attacked hosts parasitised by themselves or conspecifics. It is likely that host discrimination is absent in *C. luteum* or relies on internal cues that usually develop over time, and that the time interval between the first and subsequent ovipositions was too short to detect such cues. In our previous study (unpublished), *C. luteum* showed superparasitism even in an abundance of unparasitised hosts. It could also be suggested that the inability of *C. luteum* to discriminate between self and conspecific superparasitism is an indication that such ability may be lacking in the species. For example, Van Dijken & Waage (1987) observed a lack of self and conspecific host discrimination in the egg parasitoid *Trichogramma evanescens* Westwood. Similarly, *Aphidius matricariae* Haliday, a solitary endoparasitoid of the aphid *Myzus persicae* (Sulzer), was unable to distinguish parasitised from unparasitised hosts (Hart et al., 1978). Unfortunately, superparasitism and host discrimination in members of the genus *Coccygidium* are not known.

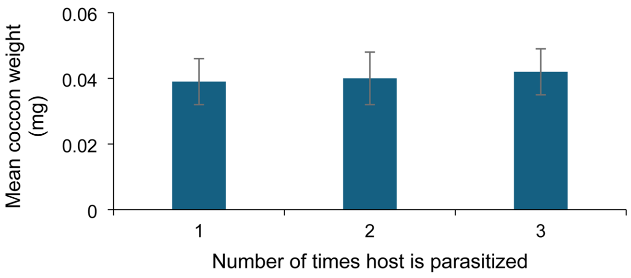

Fig. 5. Mean cocoon weight (mg) ± SE of *Coccygidium luteum* reared from *Spodoptera frugiperda* larvae that were parasitised once and from those that were superparasitised.

A major factor influencing host handling time is whether the host was previously parasitised or not. In most cases, the injection of toxins and polyhydroviruses along with parasitoid eggs not only suppresses the host's immune system, but also physically weakens the host. Mobile hosts can avoid parasitoid attacks by shaking, kicking or, in the case of lepidopteran species, dropping onto a silk thread (Hajek, 2012). Unparasitised *S. frugiperda* larvae tend to become more aggressive and defensive against predation and parasitism as they develop from one instar to another (Li et al., 2021), especially through physical fighting. This situation could explain the increase in handling time of the unparasitised larvae. It is therefore suggested that *C. luteum* may have injected host defence suppressants during the first encounter, thereby weakening the host and reducing handling time during subsequent encounters. There is considerable evidence that ovipositing parasitoids inject toxins, viroids and other substances to suppress host immunity (Amaya et al., 2005; Andrew et al., 2006). It is also possible that *C. luteum* does not lay additional eggs after internally inspecting previously parasitised hosts. While this may be true, in this study we did not dissect the larvae after each oviposition bout and therefore cannot confirm post-insertion rejection during the second and third oviposition bouts in this species. In *Pachycrepoideus vindemmiae*, handling time is reduced when females reuse previous oviposition holes (Goubault et al., 2004). While this may be true for *C. luteum*, the possibility of using previous oviposition holes in subsequent ovipositions was not examined in this study.

Superparasitism has been shown to negatively affect the developmental time of the immature parasitoid and the fitness of the progeny. Several studies have reported longer developmental times in superparasitised hosts than in unparasitised hosts. For example, superparasitism in *Ooencyrtus kuvanae* (Howard), *Chelonus oculator* Panzer, *Cotesia vestalis* (Haliday) and *Cotesia flavipes* Cameron resulted in longer developmental time (Potting et al., 1997;

Tunca & Kilinçer, 2009; Tunca et al., 2016). Harvey et al. (1993) reported that the effect of superparasitism on developmental time in *Venturia canescens* (Gravenhorst) was influenced by the host instar. However, in our study, the developmental time in superparasitised hosts was similar to that in unparasitised hosts. A similar observation was made in *C. vestalis* at low levels of superparasitism (Chen et al., 2020). Thus, the effect of superparasitism on progeny development time may be influenced by many factors, including the time interval between successive parasitisms. Some studies have reported the negative effect of superparasitism with increasing time intervals between successive ovipositions. For example, Duval et al. (2018) observed that increased time intervals between successive ovipositions had a negative effect on progeny survival. A similar observation was made in *C. vestalis*, where superparasitism beyond 12 h intervals affected the survival of the second clutch (Chen et al., 2020).

Body size is a major determinant of fitness in insects, including hymenopteran species, as it influences many life history traits. Larger female wasps of the same species are thought to handle hosts better and lay more eggs than smaller ones (King & Napoleon, 2006; Gao et al., 2016; Song et al., 2017). This suggests that the reproductive efficiency of parasitoid wasps is highly dependent on the size of female progeny. Progeny size in parasitoids is influenced by either host size or superparasitism, both of which affect the availability of nutritional resources. Superparasitism has been shown to negatively affect parasitoid size in both gregarious and solitary species (Gu et al., 2003; Santolamazza-Carbone & Rivera, 2003; Ozkan, 2006; Chen et al., 2021). In contrast, the progenies of *Aphidius ervi* Haliday from superparasitised hosts were larger than single-parasitized ones (Bai & Mackuer, 1992), while the offspring of *Pimpla turionellae* (Linnaeus) showed no significant difference in size when exposed to superparasitism (Ugur, 1986). Similarly, our study found no effect of superparasitism on the size of *C. luteum*. This may be because *C. luteum* is a koinobiont parasitoid, allowing the host to continue feeding and developing after parasitism, thereby ensuring an adequate supply of food resources for the parasitoid larvae. It is also possible that the initial or supernumerary egg was encapsulated to prevent competition between developing larvae. It is also likely that the death of the loser in the competition between the larvae occurred very early after both eggs had hatched, due to the time interval between successive parasitisms. The influence of superparasitism on progeny size may be influenced by several factors such as the parasitoid species, the host instar and the time interval between successive parasitisms.

In polyembryonic species such as *Macrocentrus grandii* Goidanich, self-superparasitism improved the sex ratio, eliminated brood failure and increased survival against conspecific larvae (White & Andow, 2008). In a related study, self-superparasitism in *Anastatus disparis* (Ruschka) resulted in a male-biased sex ratio, a situation attributed to the oviposition decision under superparasitism (Liu et al., 2021). Self-superparasitism in *Pseudapanteles dignus* (Muesebeck) was shown to evade host encapsulation in *Tuta absoluta* (*Phthorimaea absoluta*) (Meyrick) (Luna et al., 2016). While self-superparasitism may be beneficial or detrimental in parasitoids depending on the species, the main drivers of superparasitism in *C. luteum* remain unanswered. More research is needed to understand the mechanisms and drivers of superparasitism in *C. luteum*.

The results of this study show that *C. luteum* is unable to discriminate between parasitised and unparasitised hosts and therefore readily accepts the host regardless of its status. In addition, developmental time and body size were not affected by superparasitism. While the lack of host discrimination may reduce the fitness of the parasitoid through wastage of eggs and time, superparasitism during mass rearing for use in augmentative biological control does not adversely affect the quality and reproductive efficiency of *C. luteum* progenies.

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AUTHOR CONTRIBUTIONS. P. Beseh: conceptualization, design, experimentation and writing of the manuscript; B. Mensah: revision, editing and supervision; L.K. Agboyi: data analysis, revision, editing and supervision; J. Abraham: revision, editing and supervision.

DECLARATION OF CONFLICT OF INTEREST. We declare that there is no conflict of interest that may arise from the work presented in this paper.

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