



Functional and numerical responses and reproduction of *Campoletis flavicincta* parasitizing *Spodoptera frugiperda* caterpillars

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ABSTRACT. The functional and numerical responses, reproductive characteristics, and viability of *Campoletis flavicincta* (Hymenoptera: Ichneumonidae) as well as the mortality after parasitism of the host *Spodoptera frugiperda* (Lepidoptera: Noctuidae) were analyzed in the laboratory. *Campoletis flavicincta* pairs were maintained until female death with 10, 20, 30, 40, or 50 caterpillars day⁻¹ of the host *S. frugiperda*. A type III functional response curve was fitted to the average number of caterpillars supplied per day during the female wasp lifespan, as the explanatory variable. The handling time was 0.5940 ± 0.0875 h, and the instantaneous search 0.0047 ± 0.0020 h⁻¹. The functional response for each of the first five days of the host was a type III. The longevity at the five host densities and the parasitism rate showed a significant linear decrease with the host density. The offspring production showed an increasing quadratic variation with increased host density. The production of females by *C. flavicincta*, the offspring sex ratio, the viability of the parasitoid pupae and the percentage of mortality of *S. frugiperda* caterpillars were not affected by host density. The functional and numerical responses of *C. flavicincta* indicate that this parasitoid could be a candidate for biological control of *S. frugiperda*.

Keywords: fall armyworm, functional response, host density, numerical response, parasitism, parasitoid age.

Respostas funcional e numérica e reprodução de *Campoletis flavicincta* parasitando lagartas de *Spodoptera frugiperda*

RESUMO. Respostas funcional e numérica, características reprodutivas e viabilidade de *Campoletis flavicincta* (Hymenoptera: Ichneumonidae) e mortalidade após o parasitismo do hospedeiro *Spodoptera frugiperda* (Lepidoptera: Noctuidae) foram estudados em laboratório. Casais de *C. flavicincta* foram mantidos até a morte da fêmea com 10, 20, 30, 40 ou 50 lagartas dia⁻¹ do hospedeiro *S. frugiperda*. Um tipo de curva de resposta funcional III foi ajustado para o número médio de lagartas fornecidas por dia, durante a vida da vespa fêmea, como a variável explicativa. Tempo de tratamento foi $0,5940 \pm 0,0875$ h e taxa de busca instantânea 0.0047 ± 0.0020 h⁻¹. A resposta funcional para cada um dos cinco primeiros dias de fornecimento do hospedeiro foi do tipo III. Longevidade nas cinco densidades do hospedeiro e taxa de parasitismo mostraram redução linear significativa com a densidade do hospedeiro. Produção de descendentes mostrou variação quadrática crescente com a densidade crescente do hospedeiro. Produção de fêmeas de *C. flavicincta*, razão sexual de descendentes, viabilidade de pupas do parasitóide e porcentagem de mortalidade de lagartas de *S. frugiperda* não foram afetados pela densidade do hospedeiro. Respostas funcional e numérica de *C. flavicincta* indicam que esse parasitóide pode ser um candidato para controle biológico de *S. frugiperda*.

Palavras-chave: lagarta-do-cartucho, resposta funcional, densidade do hospedeiro, resposta numérica, parasitismo, idade do parasitóide.

Introduction

Spodoptera frugiperda J.E. Smith (Lepidoptera: Noctuidae) is a pest affecting economically important crops, such as cotton, maize, soybean, and sorghum (TAVARES et al., 2010a, 2011a). In Brazil, it is the most important pest affecting corn and can reduce the crop yields by approximately 34% (FIGUEIREDO et al., 2006). It has previously been controlled mainly using insecticides (TAVARES et al.,

2009, 2010b; ZANUNCIO et al., 1998). However, studies to identify and utilize natural enemies have been increasing (BATISTA-PEREIRA et al., 2006; PREZOTTI et al., 2004; SILVA et al., 2009).

The biological control of *S. frugiperda* can be carried out by releasing natural enemies, such as Braconidae, Eulophidae, Ichneumonidae and Trichogrammatidae species, which parasitize the eggs or caterpillars (HOBALLAH et al., 2004;

ZANUNCIO et al., 2008; TAVARES et al., 2011b). *Spodoptera frugiperda* caterpillars are a natural host for the larval endoparasitoid *Campoletis flavicincta* Ashmead (Hymenoptera: Ichneumonidae), which has been observed attacking these caterpillars in the field in Brazil (DEQUECH et al., 2005) (Figures 1A, B, C, D, E, and F). Although the biology of this parasitoid has been studied, a greater understanding of the host-parasitoid interactions is required to optimize its use as a biological control agent (MATOS NETO et al., 2004, 2005).

The family Ichneumonidae contains many important ecto- or endoparasitoids of immature insects that undergo complete metamorphosis (holometabolous), such as Coleoptera, Diptera, Hymenoptera, Lepidoptera, Neuroptera, and Trichoptera, as well as spiders (SOARES et al., 2006). They typically consume the entire host tissue and pupate within it (BRODEUR; BOIVIN, 2004). The symptoms of Ichneumonid parasitism are usually not very obvious, as reported for *Heteropelma scaposum* Morley (Hymenoptera: Ichneumonidae) in *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) caterpillars. However, the pupal body surface of this species frequently shows evidence of parasitoid attack by longitudinal dark spots after parasitoid entry (JOHNS; WHITEHOUSE, 2004).



Figure 1. Adult *Campoletis flavicincta* (Hymenoptera: Ichneumonidae) and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) caterpillars of the same age, parasitized (minor) or not (major) (A and B); *C. flavicincta* larvae leaving the *S. frugiperda* caterpillar and the cocoon formed (C and D); cocoon of *C. flavicincta* near the remains *S. frugiperda* (E and F).

The functional and numerical responses of parasitoids can determine the potential of a species to act as a biological control agent (FERNANDEZ-ARHEX; CORLEY, 2005). These functional responses define the parasitoid searching efficiency and provide an understanding of the host-parasitoid interactions (MONTROYA et al., 2000; GREENBERG et al., 2001). Numerical response data are used to evaluate the increase in the parasitoid population as a function of host density (MAHMOUDI et al., 2010). Although the numerical responses have been less well studied than the functional response, they too serve to evaluate the potential of a biological control agent. Basic biological data about parasitoids are necessary to develop models of host-parasitoid interactions and implement parasitoid mass rearing programs (GARIEPY et al., 2008). Most researches into the functional or numerical responses have been performed in unnatural settings, such as in field cages.

This paper reports on the functional and numerical responses and the reproductive characteristics of *C. flavicincta* parasitizing *S. frugiperda* under different host caterpillar densities.

Material and methods

Insects and experimental condition

Pairs of *C. flavicincta* were reared in the laboratory (MATOS NETO et al., 2005). They were placed in individual glass cages (12 cm diameter x 17 cm height, 1.7 liters, 866 cm² internal area) in an insect rearing facility in the Brazilian Agricultural Research Corporation (EMBRAPA Maize and Sorghum) in the Municipality of Sete Lagoas, Minas Gerais State, Brazil. Environmental conditions of $25 \pm 2^\circ\text{C}$, $70 \pm 10\%$ relative humidity (RH), and a photoperiod of 12 hours daylight were maintained throughout the study. The parasitoids received a solution of sugar (5%) and ascorbic acid (0.05%), and the host *S. frugiperda* caterpillars (three to four days old) were provided every day from five days after wasp emergence until their death (MATOS NETO et al., 2004). The host caterpillars were fed on an artificial diet (TAVARES et al., 2011c) and replaced with fresh caterpillars every 24 hours. After exposure to *C. flavicincta*, the caterpillars were individually transferred to 50 mL plastic cups containing the artificial diet.

Experiment

The individual experimental units were glass cages. Five treatments comprising daily supplies of 10, 20, 30, 40, or 50 *S. frugiperda* caterpillars were

offered to each pair of *C. flavicincta* in a completely randomized design with 10 replications. No substrate was used for the presentation of the host to the parasitoid. Each pair received the same number of hosts each day. The number of *S. frugiperda* caterpillars parasitized, the emergence of *C. flavicincta* larvae and adults, and the sex ratio of the parasitoid offspring were recorded. *Campoletis flavicincta* females that did not parasitize a caterpillar (one, zero, two, two, and three females in treatments with 10, 20, 30, 40, and 50 hosts day⁻¹, respectively) were excluded from the analysis and were not replaced by new females. Orthogonal polynomial contrasts were used to evaluate the significance of the effect of the number of caterpillars supplied (treatments) on the characteristics recorded. The linear and quadratic effects were estimated, and the third and fourth degree effects were included in fitting the models. The characteristics were analyzed relative to the lifespan of *C. flavicincta* females (SAS INSTITUTE, 1989).

Parameters analyzed and statistical analysis

Five functional responses were analyzed based on the mean daily number of hosts parasitized during the lifespan of the *C. flavicincta* females or for each of the first five days of the experiment. The mean daily parasitism rate during the lifetime of each *C. flavicincta* female was multiplied by the number of caterpillars provided daily in each treatment, thus converting the results into the mean daily values (Figure 2). The functional responses (type II or III) were initially determined using logistic regression to model the proportion of hosts parasitized as a function of the number of hosts supplied (JAMSHIDNIA et al., 2010; JULIANO, 1993; TREXLER et al., 1988). The parameters of the functional models were estimated using nonlinear regressions (FATHIPOUR et al., 2006; SAS INSTITUTE, 1989).

Results and discussion

Estimate of parameters

The logistic regression results did not allow for an adequate discrimination between the functional responses models (types II or III). Consequently, the proportion of hosts parasitized was plotted against the number of hosts supplied to determine if the slope was positive for values of hosts supplied near zero (in which case, the functional response was type II) or negative (demonstrating a type III functional response). However, this methodology proved inconclusive. Both models were therefore fitted, and the best was selected

according to the significance levels of the estimated parameters, a and Th , and of the estimated correlations between the observed and estimated values, R^2 (the determination coefficient).

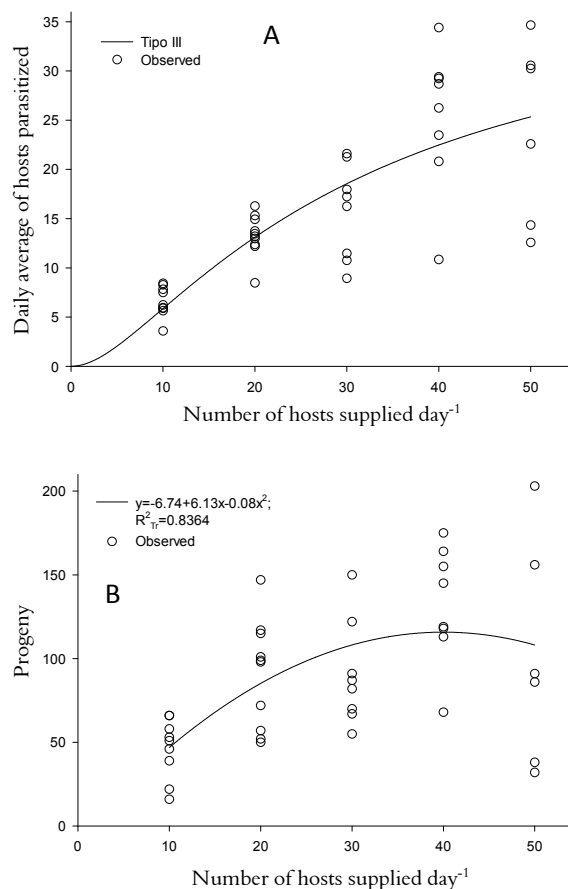


Figure 2. Functional (A) and numerical (B) responses (production of progeny) of *Campoletis flavicincta* (Hymenoptera: Ichneumonidae) females parasitizing 10, 20, 30, 40, or 50 *Spodoptera frugiperda* (Lepidoptera: Noctuidae) caterpillars at $25 \pm 2^\circ\text{C}$, $70 \pm 10\%$ relative humidity, and a photoperiod of 12L:12D.

The model selected using this method was of type III (Figure 2), with $N_p = N_o [1 - \exp(-(b \times T \times N_o \times P_t) / (1 + c \times N_o + b \times T_h \times N_o^2))]$, where N_p is the number of hosts parasitized, N_o , the number of hosts supplied, T , the available searching time (considered 24h), P_t , the parasitoid density, and T_h , the handling time, considering the lifespan of the *C. flavicincta* females. In this model, b , c , and Th are the parameters to be estimated. The instantaneous search rate (attack constant) is defined as $a = (b \times N_o) / (1 + c \times N_o)$. The estimated parameters and their associated standard errors were $b = 0.0047 \pm 0.0020 \text{ h}^{-1}$ and $Th = 0.5940 \pm 0.0875 \text{ h}$. Parameter c was discarded from the model because it was not significant ($p > 0.05$). Thus, a showed a linear variation as a function of N_o ($a = b \times N_o$), with a slope of 0.0047. The model selected for the

functional response for each of the first five days of host supply was also of type III. The handling time increased with female age, while the instantaneous search rate increased until the fourth day after the initial exposure to *S. frugiperda* caterpillars and decreased on the fifth day (Table 1).

Table 1. Estimate of the parameters (mean $\pm$ standard error) of functional response per day^a (during the first five days of host supply) of *Campoletis flavicincta* (Hymenoptera: Ichneumonidae) receiving 10, 20, 30, 40, or 50 *Spodoptera frugiperda* (Lepidoptera: Noctuidae) caterpillars at $25 \pm 2^\circ\text{C}$, $70 \pm 10\%$ relative humidity, and a photoperiod of 12L:12D.

Parameters ^b	day 1	day 2	day 3	day 4	day 5
T_h	0.2427 ± 0.0700	0.4263 ± 0.0683	0.5010 ± 0.0780	0.6682 ± 0.1240	0.4901 ± 0.1130
B	0.0035 ± 0.0012	0.0130 ± 0.0126	0.0110 ± 0.0096	0.0513 ± 0.2854	0.0060 ± 0.0038

^aHost supply beginning the fifth day after the emergence of adult parasitoids. ^b T_h is the handling time; (h) the instantaneous search rate; and (a) = $b \times N_o$ (h^{-1}) (N_o , number of hosts supplied).

Production of progeny

The numerical response (production of progeny) of *C. flavicincta* (Table 2, Figure 2) increased up to 40 hosts supplied day⁻¹ ($y = -6.74 + 6.13x - 0.08x^2$, $R^2_{Tr} = 0.8364$, $f = 9.30$, $p = 0.0005$, $df_{error} = 38$) and decreased at the highest density (50 hosts) (R^2_{Tr} is the treatment sum of squares divided by the model sum of squares).

Table 2. Effect of the number of hosts supplied (N_o) on the characteristics of the female *Campoletis flavicincta* (Hymenoptera: Ichneumonidae) parasitoids receiving 10, 20, 30, 40, or 50 *Spodoptera frugiperda* (Lepidoptera: Noctuidae) caterpillars at $25 \pm 2^\circ\text{C}$, $70 \pm 10\%$ relative humidity, and a photoperiod of 12L:12D. The decomposition of the sum of squares (SQ) of N_o in orthogonal polynomials contrasts with respective tests for lack of fit for significant contrasts.

	Characteristics						
SQ	Longevity	Progeny	Female progeny ratio	Sex ratio	Parasitism	PNV	PMH
Linear	42.36**	20483.43**	151.97 ^{ns}	0.10 ^{ns}	1040.33*	1.56 ^{ns}	11.43 ^{ns}
2 nd Degree	6.73 ^{ns}	6348.56*	93.61 ^{ns}	0.05 ^{ns}	14.99 ^{ns}	19.66 ^{ns}	0.11 ^{ns}
LOF	9.90 ^{ns}	5247.73 ^{ns}	-	-	1088.24 ^{ns}	-	-

* = $p < 0.05$; ** = $p < 0.01$; ^{ns} = Non-significant contrasts. LOF = lack of fit; PNV = percentage of non-viable parasitoid pupae; PMH = percentage of mortality of *S. frugiperda* caterpillars after exposure to the parasitoid.

Female characteristics

The longevity of *C. flavicincta* females ($y = 14.60 - 0.07x$, $R^2_{Tr} = 0.8105$, $f = 9.84$, $p = 0.0032$, $df_{error} = 39$) (Table 2, Figure 3) and the rate of parasitism of *S. frugiperda* caterpillars ($y = 70.71 - 0.37x$, $R^2_{Tr} = 0.4888$, $f = 4.14$, $p = 0.0487$, $df_{error} = 39$) (Table 2, Figure 4) showed significant linear reductions with increasing numbers of hosts supplied. However, the production of females ($f = 0.20$, $p = 0.9351$, $df_{error} = 36$), the sex ratio ($f = 1.09$, $p = 0.3774$, $df_{error} = 36$), the percentage of *C. flavicincta* pupae without adult emergence ($f = 0.66$, $P = 0.6210$, $df_{error} = 36$), and the percentage of *S. frugiperda* caterpillars

that died after exposure to the parasitoid ($f = 0.74$, $p = 0.5701$, $df_{error} = 36$), were similar at the different host densities (Table 2).

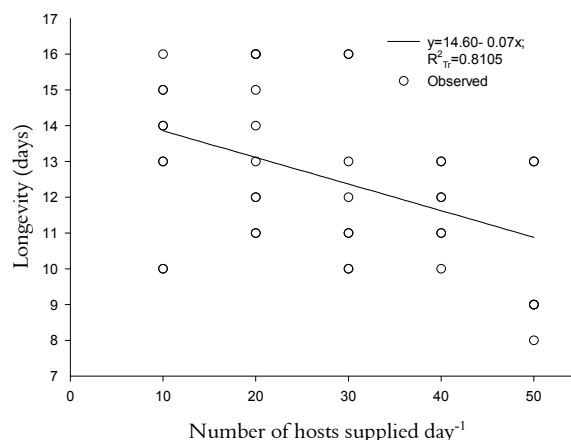


Figure 3. Longevity (days) of *Campoletis flavicincta* (Hymenoptera: Ichneumonidae) females parasitizing 10, 20, 30, 40, or 50 *Spodoptera frugiperda* (Lepidoptera: Noctuidae) caterpillars at $25 \pm 2^\circ\text{C}$, $70 \pm 10\%$ relative humidity, and a photoperiod of 12L:12D.

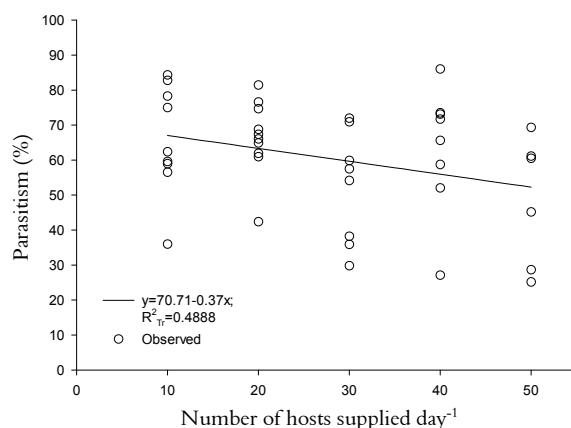


Figure 4. Parasitism (%) of *Campoletis flavicincta* (Hymenoptera: Ichneumonidae) females receiving 10, 20, 30, 40, or 50 *Spodoptera frugiperda* (Lepidoptera: Noctuidae) caterpillars at $25 \pm 2^\circ\text{C}$, $70 \pm 10\%$ relative humidity, and a photoperiod of 12L:12D.

Campoletis flavicincta showed a sigmoid functional response (type III). The instantaneous search rate, a , over the female lifespan increased linearly with the number of hosts supplied ($a = b \times N_o = 0.0047 \times N_o$ h⁻¹). The handling time (T_h) (time spent processing each food item) was 0.5940h. *Campoletis flavicincta* has high potential as a biological agent for control of *S. frugiperda* because its type III functional response suggests that its parasitism rate is density-dependent up to a certain threshold (JONES et al., 2003). Sigmoid functional responses have also been observed in other parasitoids (MONTROYA et al., 2000). They differ from the type II functional response found for *Campoletis grioti* Blanchard (Hymenoptera:

Ichneumonidae) (VARONE et al., 2007), but the different study methods used, the methods for data analysis, the arena, and the duration of the experiment may have influenced the parasitoid response (FERNANDEZ-ARHEX; CORLEY, 2005). In spite of this, the value of T_h for *C. flavicincta* (0.2427h) during the first day of host supply was similar to that observed for *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae) (0.1992h) (GREENBERG et al., 2001).

The increase in the number of progeny produced by *C. flavicincta* with host density up to 40 hosts supplied/day, and the decline in progeny production at the highest density, were similar to results obtained for *Cotesia flavipes* Cameron and *Cotesia sesamiae* Cameron (Hymenoptera: Braconidae) (SALLAM et al., 1999), but differed from those for *Glyptapanteles flavicoxis* Marsh (Hymenoptera: Braconidae), where the females produced similar numbers of progeny at different host densities (FUESTER et al., 1987). The decline in the production of progeny at the highest host density can be explained by the reduction in the number of caterpillars parasitized (considering the daily mean or total values during the female lifespan) at this density compared with at 40 caterpillars day⁻¹. For some parasitoids, this was due to increased cannibalism at the highest host density, whereby more parasitized caterpillars are consumed, leading to a decline in progeny production. The parasitized caterpillars move less (BRODEUR; BOIVIN, 2004) due to the paralyzing toxins injected by the female parasitoids during oviposition (DE MORAES; MESCHER, 2005) and/or virus (polydnavirus) transfer by the parasitoid, which can alter the host physiology making the parasitized caterpillars more susceptible to consumption by their un-parasitized counterparts (PASQUIER-BARRE et al., 2002). The fitted model showed this decline and an increase in the variability of progeny production with increasing host supply. A decrease in the production of progeny at the highest host densities has also been observed for the parasitoid *Anagyrus* sp. nov. nr. *sinope* Noyes and Menezes (Hymenoptera: Encyrtidae) when parasitizing *Phenacoccus madeirensis* Green (Hemiptera: Pseudococcidae) (CHONG; OETTING, 2007).

The longevity of *C. flavicincta* females decreased linearly with the number of hosts supplied. This suggests that females can exhaust their reproductive potential more quickly at higher host densities. Because they exhaust their reserves sooner at higher caterpillar densities, they consequently die earlier. These results are in contrast to those for *G. flavicoxis*, where female longevity was not affected by the host density (FUESTER et al., 1987). This may be because females of this parasitoid produced similar numbers of

progeny at different host densities, which did not exhaust their reserves sooner at higher densities, and longevity was consequently not affected.

The linear reduction in the parasitism of *S. frugiperda* caterpillars with increasing host density shows that there is an upper limit to the level of parasitism that *C. flavicincta* females can exert. This can be explained by egg depletion. In addition, parasitism was analyzed as a percentage and not as the numbers parasitized (Figure 3). Another possible explanation is limitations due to the handling time, which prevent a parasitoid from attacking all of the available hosts. For other parasitoids, this was explained by the reduced defensive abilities of the parasitized caterpillars, which made them more susceptible to cannibalism at higher densities (BRODEUR; BOIVIN, 2004). A reduction in the parasitism rates with increasing host density has also been reported in *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae) parasitizing Lepidoptera eggs (AYVAZ et al., 2008). Others factors besides cannibalism may be involved in the reduction of parasitism at high host densities. Host defenses against natural enemies may be more efficient when the hosts are at present higher densities. Caterpillars of Lasiocampidae and Nymphalidae feed gregariously during their initial instars, providing a behavioral protection against natural enemies (DESPLAND; HUU, 2007; INOUE; JOHNSON, 2005). In addition, *C. flavicincta* females may lay fewer eggs per *S. frugiperda* caterpillar when the host is at lower density, facilitating the ability of the caterpillars to mount immunological defenses, such as encapsulating the recently laid parasitoid eggs (BRODEUR; BOIVIN, 2004); however, the lowest density tested was 10 hosts per vial, which is still quite high.

A total of 13.2, 12.4, 16.0, 9.4, and 7.0 females were produced per *C. flavicincta* female at densities of 10, 20, 30, 40, and 50 hosts supplied day⁻¹, respectively. These averages were similar between treatments ($p > 0.05$), but the data suggest a tendency towards quadratic variation like that observed for progeny produced by *C. flavipes* and *C. sesamiae* (SALLAM et al., 1999). The sex ratio of the progeny was similar at different host densities ($p > 0.05$) but showed a tendency towards changing at higher densities, as also observed in *G. flavicoxis* parasitizing *Lymantria dispar* L. (Lepidoptera: Lymantriidae) (FUESTER et al., 1987). Thus, the numbers of female progeny, the total progeny, and the sex ratio, indicate that 10 to 30 *S. frugiperda* caterpillars should be supplied for each *C. flavicincta* female to maximize the success of mass rearing programs, depending on the laboratory resources available.

The host density did not affect the viability of *C. flavicincta* pupae or the percentage of mortality of *S. frugiperda* caterpillars. This is consistent with the results reported for *G. flavicoxis* (FUESTER et al., 1987). The mortality of *S. frugiperda* caterpillars may be due to trauma during parasitism or to superparasitism, although this was not evaluated. However, if larval mortality was due to these factors, mortality should have decreased with the increasing number of available hosts. This did not occur; suggesting that the mortality of *S. frugiperda* may be normal for this species or was caused by other factors.

The values of a and T_h for the first five days of the *C. flavicincta* female lifespan varied during this period and differed from those of a ($0.0047 \times N_0$) and T_h (0.5940) during their lifespan. This suggests that studies on the functional response should be carried out over the entire female lifespan to obtain more representative results.

Conclusion

Campoletis flavicincta showed a sigmoid functional response, demonstrating that this parasitoid can search efficiently for specific hosts at low host densities, such as those likely to occur under natural conditions. A sigmoid functional response and an increasing numerical response demonstrate good potential for use of this parasitoid in controlling *S. frugiperda* in mass or targeted releases.

Acknowledgements

The authors thank Dr. William M. Ciesla (Forest Health Management International, Fort Collins, Colorado, USA) and Dr. Simon R. Leather (Imperial College London, England) for reviewing the manuscript and “National Council for Scientific and Technological Development (CNPq)”, Coordination for the Improvement of Higher Education Personnel (CAPES), and “Foundation for Research Support of the State of Minas Gerais (FAPEMIG)” for funding this research. Asia Science Editing and American Journal Experts corrected and edited the English of this manuscript.

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Received on January 27, 2012.

Accepted on June 26, 2012.

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