

Bionomics of the acarophagous ladybird beetle *Stethorus tridens* fed *Tetranychus evansi*

K. K. M. Fiaboe^{1,5}, M. G. C. Gondim Jr², G. J. de Moraes³, C. K. P. O. Ogol⁴ and M. Knapp¹

¹African Insect Science for Food and Health (ICIPE), Nairobi, Kenya; ²Departamento de Agronomia/ Fitossanidade, UFRPE, Recife, PE, Brazil; ³Departamento de Entomologia, Fitopatologia e Zoologia Agrícola, ESALQ/USP, Piracicaba, SP, Brazil; ⁴Department of Biological Sciences, Kenyatta University (KU), Nairobi, Kenya; ⁵International Institute of Tropical Agriculture (IITA-Uganda), Kampala, Uganda

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Abstract: The bionomics of *Stethorus tridens* Gordon fed *Tetranychus evansi* Baker & Pritchard were studied in the laboratory. The number of prey consumed by *S. tridens* increased with increasing instar levels and the total mean number consumed during immature development was 184.1 ± 18.02 *T. evansi* nymphs per individual. For adult male and adult female, the daily consumption was 41.3 ± 0.80 and 67.8 ± 1.69 nymphs, respectively. *Stethorus tridens* successfully developed to adulthood between 20 and 30°C but failed at 10, 15 and 35°C. The lower thermal threshold for egg-to-adult development estimated via linear regression and the modified Logan model was 9.2 and 8.1°C, respectively. The optimum and maximum temperatures for egg-to-adult development were around 29–31 and 32.9°C, respectively. Egg to adult development time was 23.8 ± 0.24 , 17.4 ± 0.22 , 16.2 ± 0.22 and 12.1 ± 0.16 days at 20, 24, 27 and 30°C, respectively. At 27°C, the sex ratio, expressed as the proportion of females, was 0.54 and the mean preoviposition, oviposition and postoviposition periods were 10.3 ± 0.67 , 31.2 ± 4.74 and 30.2 ± 5.24 days, respectively. The oviposition rate was 4.0 ± 0.16 eggs/female/day with a female mean longevity of 71.6 ± 6.19 days and an intrinsic rate of natural increase of 0.104. The potential of *S. tridens* as a candidate natural enemy of *T. evansi* is discussed.

Key words: biological control, life table, predators, prey consumption

1 Introduction

Different predators have been reported to control mite pests. Predatory mites, mainly Phytoseiidae, are generally more effective than insect predators in controlling mites at low population levels because of various factors such as lower food requirements, short life cycle, ability to survive on alternative food sources and good host-searching ability (Huffaker et al. 1970; McMurtry et al. 1970). However, several acarophagous insects, including species of *Stethorus* Weise (Col., Coccinellidae), have been reported to feed on mite pests. All known species of the genus *Stethorus* are obligate predators of spider mites (McMurtry et al. 1970; Chazeau 1985; Rott and Ponsonby 2000; Ullah 2000) and several species have been reported to be effective biological control agents (Putman 1955; Hull et al. 1977a,b; Tanigoshi and McMurtry 1977a,b; Gotoh et al. 2004; Mori et al. 2005). They are known to be voracious predators with all motile stages feeding on all prey stages, having high host-finding and high dispersal potential, and long-living adults (Putman 1955; Tanigoshi and McMurtry 1977a,b; Roy et al. 2003, 2005).

Tetranychus evansi Baker & Pritchard is a serious exotic tomato pest in East and southern Africa (Knapp

et al. 2003; Saunyama and Knapp 2003). The mite is known to attack mainly solanaceous plant species (Blair 1983; de Moraes et al. 1987). Surveys carried out in south-eastern and north-eastern Brazil revealed various predatory mites and insects sharing the same habitat with the pest (Furtado et al. 2005; Rosa et al. 2005; Fiaboe et al. 2007).

De Moraes and McMurtry (1985, 1986) reported that *T. evansi* was unsuitable as prey for eight species of predatory mites studied. Escudero and Ferragut (2005) also reported poor performance of *Neoseiulus californicus* (McGregor) and *Phytoseiulus persimilis* Athias-Henriot on *T. evansi*. Rosa et al. (2005) found no evidence of predatory mites controlling the pest in north-eastern Brazil. *Stethorus tridens* was the most common predator found associated with the pest on solanaceous plants during surveys carried out in north-eastern and south-eastern Brazil (Fiaboe et al. 2007). The literature on *S. tridens* is limited to taxonomic reports (Gordon 1982; Gordon and Chapin 1983) and no information exists on the feeding potential, biology and effect of temperature on development of this beetle. The objective of this study was to investigate the temperature-dependent development and, in addition, to study reproduction,

longevity and prey consumption of *S. tridens* with *T. evansi* as prey.

2 Materials and Methods

2.1 Life history of *S. tridens*

In order to obtain synchronized eggs for the experiments, males and females of *S. tridens* were randomly taken from the rearing colony and confined to leaves of *Solanum americanum* Mill. infested with *T. evansi* in 17-cm-diameter arenas containing a moist sponge covered by filter paper. The arenas were closed with a lid to prevent escape of the beetles. A hole of 3 cm diameter was made in the lid and covered with a fine net to allow ventilation. The arenas were placed in incubators at 27°C, 75 ± 5% relative humidity and 12 : 12 h (light : dark) photoperiod. Twenty-four hours later, 50 eggs (replicates) were carefully collected by cutting off the section of the leaf containing the egg. Each egg was transferred to a rearing unit consisting of a Petri dish (2.5 cm in diameter and 1.5 cm height) containing two to three filter paper discs soaked with water. A leaf disc containing *S. americanum* infested with all stages of *T. evansi* was then placed on top of the filter paper discs. A hole of 1 cm diameter was made in the lid of the Petri dish and covered with a fine net to allow ventilation. Larvae were supplied daily with prey *ad libitum* by brushing mites from infested leaves into the arena. Moulting was checked daily by the presence of exuviae. Larvae were transferred to new arenas every 3–5 days, when the first signs of deterioration of the leaf disc appeared. Larvae accidentally killed in this process were not considered in the calculations.

Once the adult emerged, couples were formed (taking males from the colony maintained in a screen-house) and put in larger rearing units consisting of transparent plastic cups of 6 and 9 cm diameter at the base and top, respectively, and 13 cm height. Each contained a leaf of *S. americanum* infested with all stages of *T. evansi*. To ensure longer leaf turgidity, the petioles of the leaves were immersed in small bottles filled with water and the top of the bottle was sealed with paraffin. Observations were carried out daily until the adults died. The life-table parameters were calculated using the SAS algorithms for a jackknife procedure developed by de Maia et al. (2000).

2.2 Rate of development of *S. tridens* at different temperatures

Development of *S. tridens* was studied at seven constant temperatures (10, 15, 20, 24, 27, 30 and 35°C) using the same methodology as in the life-history study. For the calculation of survivorship, eggs were considered dead when they had shrivelled. Accidentally killed individuals were not included in the calculations. For statistical analyses of survival, individuals observed at each stage were assigned dummy variables: 1 = successfully completed the stage or 0 = died naturally during the stage. Differences in survival, with respect to temperatures and the effect of temperature on developmental time of each developmental stage as well as total development time from egg to adult were analysed by analysis of variance (ANOVA) using PROC GLM (SAS Institute 1999). In case of significant differences, mean values were separated using Student-Newman-Keuls (SNK) test at 5%.

The lower threshold (T_b) and the thermal constant (K) were estimated by simple linear regression over the linear range of the relationship between temperature (T) and

developmental rates (Y) of immature instars of *S. tridens*. Based on the equation $K = D(T - T_b)$, the linear regression equation $Y = a + bT$ obtained enabled the determination of $K = 1/b =$ thermal constant = number of degree-days required for completion of the development phase and $T_b = (-a/b) =$ lower threshold (°C), with $T =$ temperature (in°C), $D = 1/Y =$ development time (in days) (Bean 1961; Haddad et al. 1999).

The Logan model (Logan et al. 1976) modified by Lactin et al. (1995)

$$R(T) = e^{\rho T} - e^{[\rho T_{\max} - (T_{\max} - T)/\Delta]} + \lambda$$

where T is the temperature (°C), ρ , T_{\max} , Δ and λ are fitted coefficients, was used to describe the temperature-dependent development rate from egg to adult of *S. tridens*.

2.3 Prey consumption

The same methods and experimental conditions as in the construction of the life history of *S. tridens* were used here, except that only protonymphs and deutonymphs were offered as prey and the number of prey was counted. Between 30 and 40 nymphs were offered when predators were in the immature phase while approximately 200 nymphs were offered when predators were in the adult stage. Predators were transferred daily to new rearing units and the number of prey consumed was assessed deducting the number of nymphs alive from the total number offered; adults were evaluated in the same units used for immature stages and were observed for 10 days. The adult females used were all in their oviposition period. Consumption by males and females was compared using a chi-squared test.

3 Results

3.1 Life history of *S. tridens*

The newly laid eggs were whitish or reddish, becoming dark some hours before hatching. Both reddish and whitish eggs produced females and males. Each female always produced eggs of the same colour. Reddish and whitish eggs were laid by 42% and 58% of the females observed, respectively. Eggs were elongate and rounded at both ends. They were laid on the leaf disc in areas with the highest concentration of *T. evansi*. Four instars were observed. Before each moult, a sticky substance was secreted at the end of the abdomen, gluing the larva to the leaf surface. All instars possessed dark setae on the tergite and pleurite. Pupae were oval, flattened, apically enlarged, bearing fine hairs, and were always found attached to the leaf surface by their posterior extremity. They were brown in the first few hours and became darker with increasing age. The adults were oval and convex. They were light yellowish at emergence but soon became dark brown and then black.

The sex ratio as a proportion of females was 0.54. Adult survival and egg production declined as females aged, with an ovipositional peak at 17 days after adult emergence (fig. 1). The mean preoviposition, oviposition and postoviposition periods were 10.3 ± 0.67, 31.2 ± 4.74 and 30.2 ± 5.24 days, respectively. The oviposition rate was 4.0 ± 0.16 eggs/female/day (table 1). Eggs were laid intermittently and during

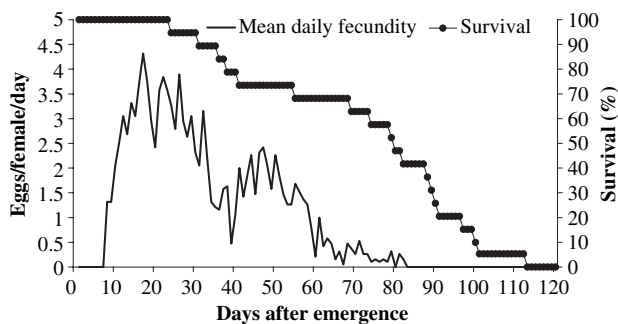


Fig. 1. Age-specific reproduction and survival of adult females of *Stethorus tridens* fed *Tetranychus evansi* at 27°C, 75 ± 5% relative humidity and 12 : 12 h (light : dark) photoperiod

the oviposition period, and females spent a mean of 7.1 ± 1.7 days without ovipositing. Variability in fecundity and longevity of the females studied was high, with daily fecundity ranging from 1 to 21 eggs/female, total oviposition from 8 to 383 eggs and longevity from 23 to 112 days. No statistical differences were found between mean longevities of females and males ($P > 0.05$). Jackknife estimates were 0.104 and 1.110 as in table 2 for r_m and λ , respectively (table 2).

Stethorus tridens successfully developed to adulthood between 20 and 30°C, but failed to complete development at 10, 15 and 35°C (table 3). At 10°C, no eggs hatched and at 15°C, only 4.6% of the eggs hatched and all larvae died during the first instar.

At 35°C, all eggs quickly darkened, a change that usually indicated that larvae were about to hatch; but only 26.7% of them hatched; 6.2% of the first instars reached the second instar but none went beyond. Survival between 20 and 30°C was higher than 85% in all stages and did not vary between temperatures (table 3).

The effect of temperature on the duration of each immature stage of *S. tridens* as well as the total development time from egg to adult was highly significant ($F = 612.3$; d.f. = 3, 130; $P < 0.0001$). Between 20 and 30°C, development time for each stage decreased with an increase in temperature (table 4).

Table 1. Different biological parameters of adult *Stethorus tridens* fed *Tetranychus evansi* at 27°C, 75 ± 5% relative humidity and 12 : 12 h (light : dark) photoperiod (n = number of adults observed)

Parameter	n	Mean ± SE
Daily fecundity per female	19	4.0 ± 0.16
Total fecundity per female	19	123.0 ± 21.46
Preoviposition period (days)	19	10.3 ± 0.67
Oviposition period (days)	19	31.2 ± 4.74
Postoviposition period (days)	19	30.2 ± 5.24
Adult female longevity (days)	19	71.6 ± 6.19
Adult male longevity (days)	11	69.5 ± 7.52

Table 2. Mean (±SE) population growth parameters of *Stethorus tridens* fed *Tetranychus evansi* at 27°C, 75 ± 5% relative humidity and 12 h photoperiod

Parameters	Jackknife estimates
Net reproductive rate (R_0)	53.231 ± 9.290
Intrinsic rate of natural increase (r_m)	0.104 ± 0.007
Mean generation time (T , in days)	38.2 ± 3.16
Doubling time (D_t , in days)	6.6 ± 0.44
Finite rate of increase (λ)	1.110 ± 0.007

For all life stages, the developmental rates increased linearly with temperature between 20 and 30°C. The linear regression of the rate of development from egg to adult on temperature was significant ($Y = -0.03504 + 0.00380T$, $R^2 = 0.94$, $F = 94.2$, $P < 0.0001$). The lower threshold temperature for development (T_b) was 9.2°C and the corresponding thermal constant 263.2 degree-days.

The modified Logan model provided a good fit for the data on egg–adult duration within the range of 15–35°C ($R^2 = 0.91$, $P \leq 0.001$; fig. 2). The fitted parameters were estimated as $\rho = 0.0037$, $T_{max} = 35$, $\Delta = 0.8906$ and $\lambda = -1.0301$. Based on this model, the lower, optimum and maximum temperatures were estimated as 8.1, 29–31 and 32.9°C, respectively.

3.2 Prey consumption of *S. tridens*

The number of nymphs consumed daily by *S. tridens* larvae increased from the first to the fourth instar (table 5). The total number of prey consumed per immature *S. tridens* was 184.1 ± 18.02 nymphs. Daily consumption was higher for females than for males ($\chi^2 = 227.02$, $P < 0.0001$).

4 Discussion

The sex ratio obtained for *S. tridens* was within the range reported for *Stethorus japonicus* Kamiya, *Stethorus picipes* Casey, *Stethorus punctum* (LeConte), *Stethorus siphonulus* Kapur, *Stethorus vagans* (Blackburn) and *Stethorus vinsoni* Kapur (Putman 1955; Moutia 1958; Raros and Haramoto 1974; Tanigoshi & McMurtry; 1977a; Ullah 2000; Mori et al. 2005).

The preoviposition period of *S. tridens* was between two and four times longer than reported for *S. vinsoni* (Moutia 1958), *S. siphonulus* (Raros and Haramoto 1974), *S. picipes* (Tanigoshi and McMurtry 1977a), *S. vagans* (Ullah 2000), and *S. japonicus* (Mori et al. 2005). However, Colburn and Asquith (1971) reported a preoviposition period of *S. punctum* twice longer than the one found in the present study.

The oviposition period of *S. tridens* was longer than in *S. siphonulus* (Raros and Haramoto 1974) and *S. vagans* (Ullah 2000), but shorter than in *S. vinsoni* (Moutia 1958), *S. picipes* (Tanigoshi and McMurtry 1977a) and *S. japonicus* (Mori et al. 2005). The intermittence in the oviposition was also reported by Moutia (1958) for *S. vinsoni*. Within the same thermal range, the daily oviposition rate of *S. tridens* is higher

Table 3. Survival (%) of the different immature instars of *Stethorus tridens* at seven constant temperatures

Life stage	Survival (%)						
	10°C (50 ¹)	15°C (65)	20°C (54)	24°C (60)	27°C (53)	30°C (55)	35°C (60)
Egg	0.0 c ²	4.6 c	87.0 a	95.0 a	96.2 a	98.2 a	26.7 b
Instar 1	*	0.0 b	85.1 a	90.2 a	100.0 a	94.2 a	6.2 b
Instar 2	*	*	92.5 a	100.0 a	100.0 a	100.0 a	0.0 b
Instar 3	*	*	97.3 a	90.3 a	94.4 a	93.9 a	*
Instar 4	*	*	97.2 a	92.9 a	91.0 a	97.8 a	*
Pupa	*	*	100.0 a	100.0 a	97.0 a	97.8 a	*
Total	*	*	64.6	71.7	80.2	83.1	*

¹Initial number of individuals.
²Mean values followed by the same letter in the same row are not significantly different (SNK; P < 0.05). For statistical analysis of the survival, individuals were assigned dummy variables of 1 (successfully completed the stage) or 0 (naturally died during the stage).

than that reported for *S. picipes* (Tanigoshi and McMurtry 1977a), but lower than that for *S. vagans* (Ullah 2000) and *S. japonicus* (Mori et al. 2005). The post-oviposition period of *S. tridens* was 2.6 to 15 times longer than that reported for *S. siphonulus* at 27–32°C (Raros and Haramoto 1974), *S. vagans* at 25–30°C (Ullah 2000) and *S. japonicus* at 25–30°C (Mori et al. 2005). In terms of prey consumption, this long lifespan is a beneficial factor for the efficiency of the predator, as this may increase the total prey consumption.

The longevity and total oviposition of female *S. tridens* were within the range reported from other *Stethorus* species at similar temperature (Moutia 1958; Chazeau 1974; Raros and Haramoto 1974; Puttaswamy and ChannaBasavanna 1977; Tanigoshi and McMurtry 1977a; Shen et al. 1999; Ullah 2000; Roy et al. 2003; Mori et al. 2005).

The r_m value obtained for *S. tridens* was lower than that reported for most other *Stethorus* species (Chazeau 1974; Tanigoshi and McMurtry 1977a; Shen et al. 1999; Roy et al. 2003; Mori et al. 2005). The intrinsic rate of increase is strongly correlated with developmental time and oviposition rate, and as the developmental time of *S. tridens* is similar to these species, the difference in r_m values can be attributed to differences in oviposition rate (Mori et al. 2005). However, the high variability in daily and total fecundity found between females in the present study suggests that prolific strains could be selected in order to improve the fertility of *S. tridens* and consequently enhance its

suitability as a natural enemy of *T. evansi* (Hopper et al. 1993).

In theory, a predator that has a population growth rate equal to or greater than its prey should efficiently regulate the population of its prey (Sabelis 1991; Roy et al. 2003). This is an important parameter in the selection of promising biological control agents. However, other parameters such as predation capacity, early host detection ability and longevity may equally contribute to the dynamics between the predator and its prey (Roy et al. 2003). Bonato (1999) reported an r_m value of 0.243 for *T. evansi* at 26°C. The capacity for population increase in *T. evansi* is therefore far higher than in *S. tridens* but one individual of the predator consumes 184 *T. evansi* nymphs during its developmental time and adult males and females consume 41 and 68 nymphs per day, respectively.

Being a tropical species, *S. tridens* had a narrower thermal range for development than *S. japonicus*, *S. punctillum* and *S. vagans* (Putman 1955; Ullah 2000; Roy et al. 2002; Mori et al. 2005), which occur in temperate climates (Gordon and Chapin 1983). The lower thermal threshold for all immature stages of *S. tridens* combined (9.2°C) was lower than the one reported for *T. evansi* (13 and 10.3°C) (de Moraes and McMurtry 1987; Bonato 1999). This suggests that *T. evansi* may not constitute a major problem at low temperatures. However, *T. evansi* was able to complete development at 36°C (Bonato 1999), while the maximum temperature estimated in the present study for *S. tridens* was 32.9°C. This suggests that at higher

Table 4. Mean developmental time (days ± SE) of *Stethorus tridens* at seven constant temperatures

Life Stages	Temperature (°C)						
	10	15	20	24	27	30	35
Egg	Did not hatch	16.3 ± 2.03 a ¹³ ²	5.9 ± 0.14 b (47)	4.0 ± 0.04 c (57)	3.9 ± 0.08 c (51)	3.0 ± 0.03 d (54)	3.0 ± 0.00 d (16)
Instar 1	*	*	3.9 ± 0.11 a (40)	2.2 ± 0.12 b (37)	2.2 ± 0.13 b (40)	1.9 ± 0.07 bc (49)	1.0 ± 0.00 c (1)
Instar 2	*	*	2.2 ± 0.10 a (36)	2.0 ± 0.15 ab (32)	1.8 ± 0.11 b (38)	1.1 ± 0.03 c (49)	*
Instar 3	*	*	2.6 ± 0.11 a (35)	2.4 ± 0.14 a (28)	2.0 ± 0.14 b (34)	1.1 ± 0.05 c (46)	*
Instar 4	*	*	4.3 ± 0.09 a (34)	3.1 ± 0.13 b (26)	3.1 ± 0.15 b (31)	2.3 ± 0.07 c (45)	*
Pupa	*	*	5.0 ± 0.03 a (34)	4.0 ± 0.06 b (26)	3.5 ± 0.16 c (30)	2.8 ± 0.07 d (44)	*
Egg–Adult	*	*	23.8 ± 0.24 a (34)	17.4 ± 0.22 b (26)	16.2 ± 0.22 c (30)	12.1 ± 0.16 d (44)	*

¹Mean values followed by the same letter in the same row are not significantly different (SNK, P < 0.05).
²Number successfully completing each corresponding life stage.

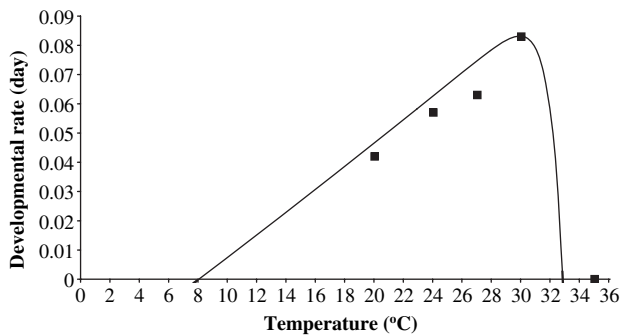


Fig. 2. Developmental rate of *Stethorus tridens* expressed as a function of temperature using the modified Logan model

temperatures, the pest population may increase rapidly in absence of the predator. The lower thermal threshold estimated by linear regression (9.2°C) was close to the value obtained from the modified Logan model (8.1°C). However, both calculated values are well below 15°C where no development occurred in the experiment. Lower thermal thresholds are more difficult to estimate than upper thresholds. More experimental work at temperatures close to the lower threshold would be required to obtain a better fit of the model (Roy et al. 2002). The population of *S. tridens* was collected in Recife, an area with high year-round temperatures. More detailed investigations on the lower threshold should be carried out in case the species is considered for classical biological control of *T. evansi* in other areas.

Various studies have been conducted to assess the feeding capacity of different *Stethorus* species but most of them used only eggs of the prey or all stages together (Putman 1955; Moutia 1958; Raros and Haramoto 1974; Hull et al. 1977a; Rott and Ponsonby 2000; Ullah 2000; Raworth 2001; Gotoh et al. 2004). Comparisons with the results obtained in this study, in which nymphs were used, are difficult. *Stethorus* species have been reported to feed on all prey stages, but have a strong preference for eggs (Houck 1991; Ullah 2000). However, the preferred prey stage varies according to the species and stage of development of the predator (Raros and Haramoto 1974; Houck 1991; Ullah 2000; Ragkou et al. 2004). Various authors demonstrated that the handling time per motile prey

Table 5. Daily consumption (mean \pm SE) of *Tetranychus evansi* nymphs by different stages of *Stethorus tridens*

Life stage	Daily consumption	
	No. predators evaluated	Mean (\pm SE)
Immatures		
Instar 1	28	8.3 \pm 0.59
Instar 2	15	13.1 \pm 1.01
Instar 3	14	17.4 \pm 0.92
Instar 4	12	29.2 \pm 2.42
Adults		
Male	9	41.3 \pm 0.80
Ovipositing female	11	67.8 \pm 1.69

was higher than that of prey eggs; and when offered all stages of prey together, more than 80% of prey consumed by adult *Stethorus* consisted of eggs (Putman 1955; Moutia 1958; Raros and Haramoto 1974; Houck 1991; Ullah 2000). On the other hand, Raros and Haramoto (1974) reported that larvae and adults *S. siphonulus* that had just fed on nymphs or adults of *Tetranychus cinnabarinus* (Boisduval) remained idle for a longer time before seeking for another prey than those that had just fed on eggs or larvae, and consequently fewer nymphs and adults were consumed than eggs, probably because nymphs and adults are larger and provide more food than eggs. Furthermore, the smaller size and the non-motile nature of the eggs compared with fast-moving nymphs, facilitate prey capture and reduce handling time. It is therefore hypothesized that the number of individuals killed by *S. tridens* adults would have been even higher if the prey stage offered had been eggs. Prey-stage preference studies need to be carried out to test this hypothesis.

The high voracity, long life span and good reproduction attributes of *S. tridens* found in the laboratory indicate that it might be an effective predator that can be used for the control of *T. evansi*. Tanigoshi and McMurtry (1977a,b) demonstrated that despite a lower intrinsic rate of increase of *S. picipes* on *Oligonychus punicae* (Hirst) compared with *Typhlodromus floridanus* (Muma), *T. floridanus* and *S. picipes* together were more effective against the pest than either predator alone. Roy et al. (2005) also reported complementarities between *S. punctillum* and *Neoseiulus fallacis* (Garman) against *Tetranychus mcDanielli* McGregor. It should therefore be tested if *S. tridens* can be more efficiently used in combination with effective predatory mites against *T. evansi* than as a stand-alone solution.

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- Author's address:** Komi K. M. Fiaboe (corresponding author), International Institute of Tropical Agriculture (IITA-Uganda), P.O. Box 7878, Kampala, Uganda. E-mail: mokfiaboe@yahoo.fr