Adult lifetime predation of *Tuta absoluta* eggs by three Neotropical mirid predators on tomato

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Abstract

Tuta absoluta (Meyrick), a key pest of tomato, is quickly spreading over the world. Here we report lifetime predation of *T. absoluta* eggs by adults of three Neotropical mirid species [*Campyloneuropsis infumatus* (Carvalho), *Engytatus varians* (Distant) and *Macrolophus basicornis* (Stal)]. Prey eggs were offered *ad libitum* on a tomato leaflet at 24 ± 1 °C, 70 ± 10% RH and 12-h photophase. Daily, the number of eggs consumed by adults was noted. Observations were terminated after all adults had died. Total adult lifetime predation of *T. absoluta* eggs was 337, 313 and 339 for males, and 845, 668 and 934 for females of *C. infumatus*, *E. varians* and *M. basicornis*, respectively. Mean adult lifespan was 27 days for males and 24 for females of *C. infumatus*, 17 days for males and 14 for females of *E. varians*, and 30 days for males and 26 days for females of *M. basicornis*. Total and daily predation was significantly higher for females than for males, though lifespan was significantly longer for males than for females. The daily predation rates of *C. infumatus* and *M. basicornis* were similar, but were significantly lower than that of *E. varians*. Predation rates tended to decrease significantly with adult age for both sexes of all three species, except for males of *M. basicornis*, although proportions of explained variance were low ($r^2 < 0.24$). Adult survival and egg predation data will later be combined with data about egg development time and survival, and nymphal development time, survival and egg predation to determine the pest kill rate of the three mirid species. The pest kill rate will then be used to predict which of the mirids might be best for control of *T. absoluta* on tomato. Eventually, experiments at practical tomato production conditions will show whether our predictions are correct.

Key words: *Campyloneuropsis infumatus*, *Engytatus varians*, *Macrolophus basicornis*, biological control, Miridae, tomato borer.

Introduction

The tomato borer *Tuta absoluta* (Meyrick) (Lepidoptera Gelechiidae), native to South America, has recently developed into a serious worldwide pest of tomato (EPPO, 2017). Due to its leaf-mining habit, chemical control is difficult. Currently, other ways of controlling this pest are studied, such as biological control (Bueno *et al.*, 2013). In Latin America and in Europe, many natural enemies were found in association with *T. absoluta*, but few of those have been evaluated and even fewer are applied for biological control of this pest (Calvo *et al.*, 2012; Zappalà *et al.*, 2013; Gabarra *et al.*, 2014; van Lenteren, 2012; van Lenteren *et al.*, 2018a). Of all types of natural enemies of *T. absoluta*, it appeared that particularly predatory mirids have been successful in controlling this tomato borer in tomato in Europe (Calvo *et al.*, 2012). Also for control of other pests, predatory mirids are increasingly used (van Lenteren *et al.*, 2018a). Due to Access and Benefit Procedures as a result of the Nagoya Protocol (Mason *et al.*, 2018), is it complicated and very time consuming to try to import European mirids into South America. However, biological control successes obtained with mirids elsewhere stimulated a search for predators of *T. absoluta* in Brazil, resulting in the finding of, among others, three Neotropical mirid predators, *Campyloneuropsis infumatus* (Carvalho), *Engytatus varians* (Distant) and *Macrolophus basicornis* (Stal) (Hemiptera Miridae) (Bueno *et al.*, 2013).

Results obtained for these three Neotropical mirids indicate that they might be promising candidates for control of *T. absoluta* and other tomato pests: they quickly establish populations on tomato (Bueno *et al.*, 2013), and show high predation rates in the laboratory (van Lenteren *et al.*, 2016). Predatory mirids often feed on plant material and are, therefore, categorized as zoophytophagous (Bueno and van Lenteren, 2012). Plant feeding can be beneficial, resulting in survival of the predator during periods with low prey populations, as well as detrimental by causing injury to the plant or fruits (Castañé *et al.*, 2011). We have studied the phytophagous behaviour of the three Neotropical mirids and found very limited injury to tomato plants and fruit in the laboratory (Silva *et al.*, 2016a), as well as in a greenhouse experiment (van Lenteren *et al.*, 2018b). Thus, contrary to the serious plant and fruit damage that may be caused by mirids used for *T. absoluta* control in Europe (Calvo *et al.*, 2009), the mirids we tested seem much less problematic with regard to phytophagy, and we will, therefore, not discuss this phenomenon later in this paper.

To date, surprisingly little biological information is available for both the Neotropical and the European mirid species used in biological control programmes. One of the lacking points of information concerns the lifetime predation capacity of mirids. Lifetime predation data are important to select the most promising natural enemy and terminate research on less promising species

(van Lenteren, 2010), but also for developing mass rearing methods and field and greenhouse release programmes. Some predation data have been published for three European mirid species (Abbas *et al*., 2014; Mollá *et al*., 2014) and for the three Neotropical species mentioned above (van Lenteren *et al*., 2017). Results published by these authors only concern nymphal predation. Data published by van Lenteren *et al*. (2016) relate to 24h adult predation, but these are of limited value as they are short-term measurements over one day, and, due to a period of starvation before the test, tend to overestimate overall adult predation. Thus, the currently available data are insufficient to estimate lifetime predation for these mirids.

In this paper, we report data about adult lifespan, and daily and total predation by males and females of three Neotropical mirid species, *C. infumatus*, *E. varians* and *M. basicornis*, when offered eggs of *T. absoluta ad libitum* on tomato. Our eventual aim is to hypothesize about the biological control efficiency of these three mirids based on earlier published data on survival, development time, sex ratio and nymphal predation (van Lenteren *et al*., 2017), together with results obtained during this study on adult predation, before greenhouse or field experiments under practical conditions are performed.

Materials and methods

Collection and rearing of *Tuta absoluta*

Eggs, larvae and pupae of *T. absoluta* were collected from tomato plants at the experimental area of the campus of the Federal University of Lavras, Minas Gerais, Brazil (21°14'43"S 44°59'59"W, 919 m a.s.l.) in 2010. Newly emerged adults from these collections were released in a mesh cage (70 × 70 × 50 cm) with unsprayed tomato plants (*Solanum lycopersicum* L. cv. IPA-6) in a climate room at 25 ± 2 °C, RH 70 ± 10% and a photoperiod of 14h light/10h dark. Adults were allowed to oviposit for three days and were then removed. Newly emerged adults from these cages were used to start the rearing of the next generation.

Collection and rearing of the mirid predators

First surveys for mirid predators were done in the municipality of Ribeirão Vermelho, Minas Gerais State, Brazil (Brazil 21°11'26"S, 45°03'43"W, 808 m a.s.l.) from 2010 to 2013. Collection, identification and maintenance of stock rearings of the three mirid predators on unsprayed tobacco plants (*Nicotiana tabacum* L. cv. TNN) and eggs of *Ephestia kuehniella* Zeller as food are described in Bueno *et al*. (2012; 2013). For the current experiment, new predators were collected at the above-mentioned locality, and kept for 1-3 generations on tobacco plants cv. TNN with eggs of *E. kuehniella* as food in mesh cages (70 × 70 × 50 cm) in a climate room at 24 ± 1 °C, RH 70 ± 10% and 12-h photophase. The rearings on tobacco were started with at least 100 field collected adult mirids of each species, and each new laboratory generation was started with at least 200 adult mirids. Adult predators collected from the rearings on tobacco were transferred to new cages containing un-

sprayed tomato plants (cv. Santa Clara), and after nymphal emergence, *E. kuehniella* eggs were added twice a week. These rearings on tomato were kept in a climate room at 24 ± 1 °C, RH 70 ± 10% and 12-h photophase and adult predators from the second generation on tomato were used in the experiments.

Total egg predation by mirid adults

Data about adult predation by the three mirids from Smit (2015) and van Lenteren *et al*. (2016) were used to estimate the maximum number of *T. absoluta* eggs that adults could consume per day. The daily numbers of prey eggs offered to a couple of adult was 160, and to single adult males and single adult females was 60 and 100, respectively. Tomato leaflets were introduced into rearing cages with many *T. absoluta* adults for egg laying during 24h. In case leaflets had insufficient eggs, additional *T. absoluta* eggs were put on the tomato leaflet after carefully removing them from plants of the stock rearing with a wet paint brush.

Single, unsprayed tomato leaflets with the required number of prey eggs were then placed with their stem in Eppendorf tubes (1.5 ml) filled with a 1% agar-water suspension to prevent wilting, and then put in a Petri dish (9 cm diameter) together with a newly emerged couple of adult predators. Predation by a couple of predators was measured for 7 days. We had to use this methodology because mating of mirids may take place during the first seven days of adult life (Castañè *et al*., 2007). After 7 days, males and females were separated, and predation of single males and single females was determined until they died. Daily, after a 24h-interval, the number of eggs consumed was counted under a stereomicroscope at 30× magnification. Collapsed and totally empty eggs were considered to have been consumed by the adult mirids. After counting and noting the condition of the adults (alive or dead), a new leaflet with eggs substituted the previous one. The number of replicates was 20 for each of the three mirid species. The experiment was carried out in a climate room at 24 ± 1 °C, 70 ± 10% RH and 12-h photophase.

In order to be able to obtain lifetime predation data of males and females separately, we used the following method to estimate predation by the two sexes during the first 7 days. First, we calculated daily predation by males and females during day 8-17, i.e. the first 10 days after males and females were separated. We used this period to obtain sufficient replicates and to prevent the effect of diminishing egg predation rates at the end of the adult life of mirids. Next, the total number of *T. absoluta* eggs eaten by males and females during these 10 days was used to calculate the percentages eggs eaten by the two sexes. The percentages (about 75% of the eggs were eaten by females and 25% by males) were then applied to the predation rates of couples during the first 7 days. Detailed tables illustrating the above-mentioned procedure are provided in supplemental material (tables S1-S4).

Data analysis

All analyses were performed with the complete lifetables obtained after the procedure described in the section above. Separate analyses were performed for the

response variables "duration of developmental stage" and "number of eggs consumed". The aim was to test for any differences between the species of predators, and the sexes, respectively. Separate univariate, fixed factor, two-way generalized linear models (GLMs) were performed, assuming that the two response variables had equal variances and were normally distributed. The latter was confirmed to be the case for the number of eggs consumed per species separately, but not entirely for the duration of developmental stage (Kolmogorov-Smirnov test for normality). Post-hoc tests were performed where the model explained a significant proportion of the variation, and where the factor "species of predator" contributed significantly to the variation, where the Sidak method was applied to adjust the significance level. We performed separate one-way univariate GLMs per species to detect whether within each species, males and females differed in total and daily egg-consumption during the adult period. To determine if there was any trend in egg consumption over time, we performed six least squares linear regression analyses (one for each sex of each species), where we weighted each data point by the number of individuals that was still alive at that time. Thus, in the regression, data points at the beginning of the experiment (when many insects were still alive) received a higher weight than towards the end of the experiment (when many individuals had already died), to prevent any bias caused by stochasticity especially towards the end of the experiment, when egg-consumption was estimated based on a limited number of individuals. All above analyses were performed using IBM SPSS statistics version 22.

For the longevity of adults, we visualized the data and we drew Kaplan-Meier survivor plots. The differences between sexes and species were first tested with an overall Log-rank test. Thereafter, we performed a parametric survival analysis (Kleinbaum and Klein, 2006) for exponential or Weibull distributed survival times to assess the effects of species and sex. The exponential distribution is a special case of the Weibull distribution with shape parameter $k = 1$. For both distributions the baseline hazard function $h(t)$ at time t is known (equation 1):

$$h_0(t) = \frac{k}{\lambda} \left(\frac{t}{\lambda} \right)^{k-1} \qquad (1)$$

Here the baseline hazard rate $h_0(t)$ is for the females of the species $C.\ infumatus$, and represents the instantaneous mortality rate at time t, given that insects were still alive before time t. The scale parameter λ occurs in both the exponential and the Weibull baseline hazard rate. For an exponential distribution this rate is constant, namely $1/\lambda$. The effects of species and sex are incorporated with a multiplication factor for the baseline hazard rate, to get the species and sex specifics hazard rate:

$$h(t) = \frac{k}{\lambda} \left(\frac{t}{\lambda} \right)^{k-1} \exp\left(k \left(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \right) \right) \qquad (2)$$

The regression coefficients β_1, β_2 and β_3 represent the influence of being $E.\ varians$, $M.\ basicornis$ or male on the mortality rate, for the binary covariates x_1 (0 = $C.\ infumatus$ or $M.\ basicornis$; 1 = $E.\ varians$), x_2 x_1

(0 = $C.\ infumatus$ or $E.\ varians$; 1 = $M.\ basicornis$) and x_3 (0 = female; 1 = male). All survival analyses were performed using R 3.1.2 (R Core Team, 2016).

Results

Adult survival and predation data

$Tuta\ absoluta$ mortality after transferring eggs with a paint brush from the stock rearing to a tomato leaflet in absence of the predators was negligible during the 24h test period: more than 10.000 eggs were checked and percentages of dead eggs due to handling or to natural mortality in the control treatments ranged from 0 to 1.12% (van Lenteren $et\ al.$, 2016). Because of this very low mortality in the control treatments, we have not corrected the predation data for "natural and handling mortality".

As explained before we had to use a special experimental set-up to obtain mated females. In supplemental material we illustrate step by step the procedure resulting in the daily predation rates during adult life female and male predators which are presented in table 1.

The daily average predation rates by males and females of the three species of mirids are presented in figures 1-3. Similarities and differences in predation rates will be described below.

Homogeneity and variance of data

Homogeneous (same species, same sex) groups were tested for normality of data for each of the three response variables 'total lifetime number of eggs consumed', and 'number of eggs consumed per day', using a Kolmogorov-Smirnov test (IBM-SPSS statistics 22). From the 18 tests done, only two deviated marginally significantly from a normal distribution, and therefore normality of the data was assumed. Variances were similar across groups within each response variable. Table 2 summarizes the data calculated from life tables per sex per species.

GLM analysis

A univariate GLM with fixed factors "species" and "sex", performed on each of the two response variables showed that the variation in total number of eggs was significantly affected by the sex, but not by the factor "species" (table 3). The estimated daily rate of egg consumption was significantly affected by species as well as sex, and their interaction (table 3).

A post-hoc test with Bonferroni correction for the response variable 'eggs/day' across species showed that the number of consumed eggs per day of $E.\ varians$ was significantly higher than that of $C.\ infumatus$ as well as of $M.\ basicornis$ ($p < 0.001$), but did not differ between $C.\ infumatus$ and $M.\ basicornis$ ($p = 0.19$).

Trends in egg predation rates over time

A regression analysis was performed on egg predation through time for each sex of each species separately (figures 1-3). Data points were weighted for number of surviving predators at that time (figures 1-3). In all, except one regression (males $M.\ basicornis$), a significant

Table 1. Adult lifetime predation of *T. absoluta* eggs by females, males and couples of *C. infumatus*, *E. varians* and *M. basicornis* on tomato at 24 ± 1 °C, 70 ± 10% RH and 12-h photophase; f = female, m = male, c = couple.

Campyloneuropsis infumatus

Replicates	1 f	1 m	1 c	2 f	2 m	2 c	3 f	3 m	3 c	4 f	4 m	4 c	5 f	5 m	5 c	6 f	6 m	6 c	7 f	7 m	7 c	8 f	8 m	8 c	9 f	9 m	9 c	10 f	10 m	10 c
Day 1	2	1	3	32	10	42	59	19	78	36	11	47	30	10	40	47	15	62	9	3	12	38	12	50	15	5	20	41	13	54
2	40	12	52	39	12	51	29	9	38	47	15	62	46	15	61	49	15	64	30	10	40	42	13	55	42	13	55	43	13	56
3	32	10	42	48	15	63	40	13	53	48	15	63	58	18	76	42	13	55	66	21	87	59	19	78	61	19	80	70	22	92
4	40	12	52	68	22	90	21	6	27	61	19	80	55	17	72	34	11	45	61	19	80	53	17	70	51	16	67	68	21	89
5	27	8	35	60	19	79	17	6	23	75	24	99	62	20	82	46	14	60	59	18	77	43	14	57	17	5	22	49	15	64
6	47	15	62	78	24	102	14	4	18	53	17	70	32	10	42	27	9	36	44	14	58	62	19	81	53	17	70	39	12	51
7	27	8	35	85	27	112	18	6	24	61	19	80	65	20	85	35	11	46	48	15	63	33	11	44	24	8	32	55	17	72
8	49	0	49	52	4	56	26	2	28	54	3	57	58	4	62	32	6	38	60	10	70	42	9	51	88	25	113	48	18	66
9	27	5	32	58	5	63	13	4	17	63	16	79	45	14	59	41	10	51	60	14	74	44	18	62	37	17	54	45	9	54
10	23	12	35	55	7	62	19	10	29	51	24	75	48	15	63	33	33	66	39	10	49	30	25	55	73	9	82	54	15	69
11	15	1	16	57	10	67	19	18	37	43	14	57	41	7	48	18	34	52	54	11	65	23	23	46	58	17	75	49	13	62
12	32	16	48	50	6	56	14	17	31	72	4	76	48	9	57	29	41	70	20	18	38	28	19	47	61	30	91	57	10	67
13	50	11	61	1	3	4	6	15	21	24	14	38	62	5	67	13	46	59	11	17	28	5	20	25	8	15	23	61	12	73
14	25	2	27	0	0			12	12	40	15	55	68	6	74	25	38	63	37	15	52	10	15	25	10	6	16	25	2	27
15	41	1	42					3	3	22	20	42	29	5	34	31	30	61	22	9	31	29	11	40	13	12	25	60	0	60
16	49	12	61					3	3	39	10	49	20	12	32	22	12	34	36	15	51	15	10	25	42	7	49	55	2	57
17	30	17	47					13	13	57	5	62	20	11	31	22	0	22	38	8	46	38	13	51	64	0	64	29	0	29
18	42	1	43					13	13	46	10	56	27	4	31	18	0	18	12	18	30	13	10	23	32	0	32	13	0	13
19	32	19	51					10	10	0	17	17	34	18	52	20	0	20	29	0	29	12	9	21	19	0	19	20	0	20
20	13	5	18					3	3		12	12	32	10	42	23		23	12		12	3	5	8	18		18	34		34
21	51	17	68					5	5		23	23	27	22	49	46		46	17		17	2	7	9	46		46			
22	32	15	47					0	0		20	20	21	15	36	17		17	8		8	6	16	22	64		64			
23	50	11	61								10	10	4	2	6			6	27		27	5	14	19	21		21			
24	25	20	45								12	12	2	1	3	0		0	7		7	20	16	36	40		40			
25	4	23	27								23	23	0	0		9		9	19		19	4	9	13	58		58			
26	0	16	16								14	14	0	0		26		26	16		16	4	2	6	33		33			
27		5	5								4	4				17		17	2		2	30	20	50	49		49			
28		12	12								10	10				30		30	8		8	28	18	46	40		40			
29		4	4								26	26				35		35	9		9	19	14	33	43		43			
30											18	18				46		46	10		10	25	17	42	20		20			
31											8	8				32		32	8		8	28	13	41	0		0			
32											4	4				37		37	18		18	2	16	18						
33											6	6				37		37	5		5	21	8	29						
34											8	8				30		30				1	20	21						
35											4	4				19		19				3	7	10						
36											24	24				14		14					16	16						
37											50	50				9		9					5	5						
38											19	19				24		24					7	7						
39											19	19				21		21					7	7						
40											14	14				9		9					4	4						
41											7	7				14		14												
42											10	10				9		9												
43											4	4				13		13												
44											11	11				6		6												
45											9	9				16		16												
46											24	24				25		25												
47											7	7				31		31												
48																19		19												
49																24		24												
50																26		26												
51																20		20												
52																17		17												
53																14		14												
54																17		17												
55																15		15												
56																13		13												
57																1		1												

Replicates	11 f	11 m	11 c	12 f	12 m	12 c	13 f	13 m	13 c	14 f	14 m	14 c	15 f	15 m	15 c	16 f	16 m	16 c	17 f	17 m	17 c	18 f	18 m	18 c	19 f	19 m	19 c	20 f	20 m	20 c
Day 1	31	10	41	43	14	57	38	12	50	23	7	30	38	12	50	29	9	38	84	26	110	59	19	78	59	19	78	65	20	85
2	74	24	98	55	17	72	55	18	73	42	13	55	54	17	71	36	12	48	54	17	71	35	11	46	65	20	85	46	14	60
3	55	18	73	49	15	64	61	19	80	26	8	34	74	23	97	46	14	60	41	13	54	45	14	59	59	18	77	55	18	73
4	55	17	72	37	12	49	46	15	61	27	8	35	0	30	30	35	11	46	54	17	71	52	17	69	85	27	112	49	15	64
5	42	13	55	32	10	42	43	13	56	24	7	31	0	36	36	46	14	60	59	18	77	55	18	73	57	18	75	47	15	62
6	58	18	76	30	10	40	32	10	42	14	4	18	0	20	20	38	12	50	63	20	83	54	17	71	32	10	42	32	10	42
7	40	13	53	25	8	33	76	24	100	6	2	8	0	12	12	35	11	46	58	18	76	80	25	105	51	16	67	19	6	25
8	40	1	41	23	0	23	61	1	62	30	20	50		11	11	70	16	86	80	5	85	45	10	55	49	16	65	45	10	55
9	29	0	29	37	0	37	48	8	56	55	22	77		23	23	24	24		78		80		26		58	18	44	62	3	51
10	8	0	8	65	0	65	28	0	28	63	21	84		14	14	49	20	69	52	4	56		4		32	12	44	62	17	79
11		20	20	35	8	43	32		32	58	22	80		14	14	34	0	34	51	0	51	87	0	87	30	4	34	46	15	61
12		12	12	5	5	25	25	52		52	17	17	58	0	58	87	0	87	0	0		52	6	58	60	17	77			
13				2	2	51	51	46	10	56	28	28	56	0	56	79	4	83	11	11	24	1	25	55	24	79			
14				20	20	50	50	33	11	44	11	11	31	30	61	16	16	67	17	84	52	30	82						
15				20	20	26	26	24	26	50	11	11	31	30	61	28	22	50	27	27	44	18	62	30	8	38			
16				19	19	25	25	28	25	53	13	13	21	30	51	5	12	17	3	3	43	8	51	40	7	47			
17				0	0	10	10	25	8	33	20	20	33	23	33	4	9	13	21	21	57	3	60	50	11	61			
18				13	13	24	24	18	12	30	27	27	50	12	62	1	14	15	23	23	67	7	74	12	11	23			
19				19	19	29	29	16	3	19	8	8	76	0	2	2	25	25	61	15	76	27	26	53						
20				2	2	33	33	46		46	9	9	47	0	47	2	2	20	20	49	12	61	20	9	29			
21							17	17	20		20	21	21	55	17	72	2	2	17	17	14	19	33	10	10	20			
22							15	15	27		27	19	19	18	16	34	5	5	21	21	43	7	50	9	11	20			
23							20	20	31		31	27	27	21		21	11	11	26	26	46	2	48	48	5	53			
24							9	9	34		34	2	2	19		19	13	13	24	24	57	2	59	16	3	19			
25									38		38	8	8	32		32	9	9	23	23	33	27	60	35	17	52			
26									29		29	26	26	30		30	6	6	14	14	42	18	60	32	9	41			
27									35		35	25	25	22		22	5	5	9	9	50	21	71	21	5	26			
28									35		35	8	8	24		24	8	8	9	9	25	3	28	20	20	40			
29									50		50	13	13	16		16	6	6	13	13	9	2	11	11	10	21			
30									31		31	10	10	14		14	9	9	6	6	0	3	3	6	3	9			
31									4		4	9	9	12		12	3	3	8	8	15	15		0	0				
32									20		20	7	7	13		13	0	0	31	31									
33									21		21	0	0	33		33													
34									31		31	18	18	35		35													
35									28		28	13	13	34		34													
36									20		20	8	8	0		0													
37									16		16	5	5																
38									10		10	4	4																
39									28		28	5	5																
40									0		0	3	3																
41												8	8																
42												20	20																

(Table 1 continued)

Replicates	f 11	m 11	c 11	f 12	m 12	c 12	f 13	m 13	c 13	f 14	m 14	c 14	f 15	m 15	c 15	f 16	m 16	c 16	f 17	m 17	c 17	f 18	m 18	c 18	f 19	m 19	c 19	f 20	m 20	c 20
Day 43														6	6															
44														0	0															
45														26	26															
46														29	29															
47														25	25															
48														20	20															
49														13	13															
50														16	16															
51														5	5															
52														21	21															
53														20	20															
54														9	9															
55														14	14															
56														18	18															
57														10	10															
58														0	0															

Engytatus varians

Replicates	f 1	m 1	c 1	f 2	m 2	c 2	f 3	m 3	c 3	f 4	m 4	c 4	f 5	m 5	c 5	f 6	m 6	c 6	f 7	m 7	c 7	f 8	m 8	c 8	f 9	m 9	c 9	f 10	m 10	c 10
Day 1	18	7	25	3	1	4	57	20	77	12	4	16	24	9	33	33	12	45	34	12	46	37	13	50	58	20	78	30	10	40
2	36	13	49	52	18	70	68	24	92	55	20	75	69	24	93	51	18	69	60	21	81	25	9	34	35	13	48	40	14	54
3	82	29	111	53	19	72	72	26	98	87	31	118	59	21	80	71	25	96	58	20	78	38	13	51	64	23	87	78	28	106
4	66	24	90	64	23	87	52	0	52	35	12	47	69	24	93	60	21	81	52	19	71	18	6	24	38	14	52	35	13	48
5	84	30	114	33	12	45	41	0	41	48	17	65	72	25	97	52	18	70	73	26	99	32	11	43	72	25	97	51	18	69
6	63	23	86	29	10	39	1	0	1	0	26	26	61	22	83	22	8	30	44	16	60	63	23	86	75	26	101	40	14	54
7	55	19	74	26	9	35	0	0	0	0	2	2	80	28	108	78	28	106	72	26	98	63	23	86	79	28	107	56	20	76
8		18	18	34	0	34				0	0		9	13	22	68	24	92	75	35	110	77	0	77	79	7	86	3	33	36
9		20	20	29		29							1	23	24	69	14	83	80	22	102	79		79	79	18	97		21	21
10		24	24	41		41							2	36	38	87	29	116	85	24	109	84		84	61	26	87		31	31
11		18	18	39		39							2	30	32	67	13	80	80	20	100	79		79	51	24	75		17	17
12		16	16	49		49							0	32	32	76	16	92	84	36	120	90		90	71	28	99		35	35
13		5	5	58		58								11	11	44	13	57	74	13	87	9		9	63	18	81		33	33
14		17	17	65		65								18	18	51	18	69	73	6	79	40		40	66	30	96		31	31
15		20	20	69		69								16	16	59	12	71	75	0	75	78		78	66	2	68		25	25
16		1	1	51		51								18	18	18	10	28	72	16	88	46		46	62		62		34	34
17		1	1	42		42								20	20	53	23	76	4	19	23	86		86	71		71		30	30
18		0	0	57		57								13	13	1	29	30	0	18	18	52		52						
19				27		27								15	15	1	36	37	0	26	26	76		76						
20				1		1								22	22	1	24	25		30	30	74		74						
21														25	25		21	21		26	26	75		75						
22														23	23		10	10		26	26	72		72						
23														1	1		18	18		14	14	52		52						
24																	12	12		36	36	66		66						
25																	16	16		40	40	40		40						
26																	18	18		30	30	14		14						
27																	7	7		6	6	2		2						
28																	12	12		2	2	0		0						
29																	9	9												
30																	31	31												
31																	11	11												
32																	5	5												
33																	10	10												
34																	12	12												
35																	9	9												
36																	0	0												

Replicates	f 11	m 11	c 11	f 12	m 12	c 12	f 13	m 13	c 13	f 14	m 14	c 14	f 15	m 15	c 15	f 16	m 16	c 16	f 17	m 17	c 17	f 18	m 18	c 18	f 19	m 19	c 19	f 20	m 20	c 20
Day 1	20	7	27	30	10	40	32	11	43	38	14	52	24	9	33	24	9	33	15	6	21	1	1	2	47	17	64	44	16	60
2	88	31	119	61	21	82	54	19	73	63	23	86	64	23	87	56	20	76	67	24	91	43	15	58	49	17	66	54	19	73
3	77	27	104	68	24	92	53	19	72	66	23	89	87	31	118	86	31	117	52	19	71	85	30	115	67	24	91	70	25	95
4	78	28	106	80	28	108	30	0	30	77	28	105	78	28	106	89	31	120	88	31	119	74	26	100	52	18	70	88	31	119
5	98	35	133	68	0	68	28	0	28	51	18	69	83	29	112	41	15	56	80	29	109	75	27	102	34	12	46	101	36	137
6	75	26	101	46	0	46	15	0	15	47	17	64	32	12	44	61	21	82	78	28	106	64	23	87	83	29	112	77	28	105
7	77	27	104	43	0	43	25	0	25	60	21	81	76	27	103	70	25	95	103	36	139	25	9	34	0	26	26	24	8	32
8	49	8	57	73		73	67		67	53	22	75	0	19	19	75	10	85	79	19	98	14	11	25		9	9	39	7	46
9	2	20	22	70		70	46		46	10	27	37		8	8	25	30	55	80	1	81	33	22	55		10	10	2	11	13
10	1	8	9	77		77	39		39	2	29	31		13	13	33	25	58	82	7	89	13	23	36		5	5	0	12	12
11		12	12	67		67	21		21		18	18		22	22	23	32	55	37	0	37	3	34	37		24	24		13	13
12		23	23	79		79	22		22		19	19		9	9	28	11	39	10	0	10	28	13	41		29	29		10	10
13		24	24	80		80	28		28		0	0		21	21	35	22	57	12		12	31		31		20	20		15	15
14		20	20	80		80	29		29		20	20	11	14	25	17		17				32	0	32		28	28		20	20
15		10	10	15		15	18		18		10	10	23	10	33	2		2				22	0	22		21	21		12	12
16		17	17	27		27	17		17		15	15	12	9	21	13		13				10		10		18	18		34	34
17		25	25	0		0	33		33		23	23	5	13	18	21		21				7		7		33	33		24	24
18		2	2	20		20	31		31				0	20	20	28		28								19	19		27	27
19				19		19	7		7					31	31	3		3								12	12		21	21
20				22		22	3		3							45		45								14	14		23	23
21				31		31	10		10							16		16								1	1		5	5
22				25		25	0		0							16		16											17	17
23				1		1										25		25											8	8
24				12		12										12		12											2	2
25																13		13											2	2
26																9		9											1	1
27																20		20											0	0

Macrolophus basicornis

Replicates	f 1	m 1	c 1	f 2	m 2	c 2	f 3	m 3	c 3	f 4	m 4	c 4	f 5	m 5	c 5	f 6	m 6	c 6	f 7	m 7	c 7	f 8	m 8	c 8	f 9	m 9	c 9	f 10	m 10	c 10
Day 1	22	7	29	30	9	39	30	9	39	34	10	44	47	14	61	47	14	61	46	14	60	25	7	32	35	11	46	57	17	74
2	31	10	41	44	13	57	35	11	46	43	13	56	51	15	66	58	18	76	41	13	54	48	15	63	20		20	43	13	56
3	44	13	57	45	14	59	48	14	62	40	12	52	48	12	60	51	16	67	41	13	54	31	9	40	23		23	32	10	42
4	50	15	65	39	12	51	72	22	94	40	12	52	51	15	66	27	8	35	55	17	72	27	8	35	17		17	39	12	51
5	42	13	55	63	19	82	58	17	75	67	21	88	39	12	51	28	9	37	48	15	63	22	7	29	10		10	51	16	67
6	48	15	63	57	17	74	57	17	74	57	17	74	42	13	55	22		22	48	15	63	36	11	47	10		10	51	15	66
7	41	13	54	32	10	42	44	13	57	45	14	59	36	11	47	13		13	54	17	71	41	13	54	7		7	27	8	35
8	36	11	47	48	5	53	32	1	33	48	15	63	64	23	87	9		9	41	10	51	37	0	37	8		8	76	8	84
9	35	13	48	20	1	21	37	7	44	43	10	53	39	19	58	21		21	41	12	53	24	1	25	16		16	82	8	90
10	31	15	46	43	10	53	21	3	24	37	19	56	59	10	69	19		19	57	19	76	10	8	18	27		27	31	0	31
11	44	9	53	39	17	56	56	17	73	25	11	36	51	19	70	12		12	50	22	72	42	8	50	13		13	71	0	71

(Table 1 continued)

Replicates	f1	m1	c1	f2	m2	c2	f3	m3	c3	f4	m4	c4	f5	m5	c5	f6	m6	c6	f7	m7	c7	f8	m8	c8	f9	m9	c9	f10	m10	c10
12	41	12	53	50	8	58	26	10	36	43	15	58	49	31	80	12	12		48	18	66	55	9	64	25		25	51	0	51
13	55	7	62	29	7	36	34	8	42	41	12	53	72	14	86	10	10		40	10	50	41	4	45	19		19	28		28
14	15	5	20	36	9	45	37	9	46	56	14	70	53	9	62	11	11		62	9	71	32	5	37	13		13	28		28
15	36	3	39	47	10	57	52	10	62	57	10	67	56	20	76	18	18		42	7	49	34	8	42	8		8	44		44
16	45	12	57	46	12	58	44	10	54	49	15	64	44	5	49	10	10		28	7	35	20	22	42	8		8	50		50
17	46	6	52	47	15	62	51	12	63	45	15	60	52	17	69	12	12		9	11	20	17	22	39	2		2	38		38
18	47	2	49	45	14	59	7	10	17	51	11	62	51	3	54	20	20		33	11	44	2	19	21	0		0	26		26
19	30	7	37	46	11	57	1	6	7	37	10	47	63	21	84	18	18		55	8	63	0	7	7				30		30
20	40	2	42	32	14	46	10		10	41	7	48	42	18	60	14	14		37	12	49	5		5				50		50
21	30	2	32	33	8	41	10		10	56	7	63	52	14	66	14	14		29	9	38	2		2				46		46
22	35	1	36	47	3	50	12		12	50	15	65	51	10	61	15	15		44	11	55	6		6				47		47
23	47	4	51	55	2	57	12		12	55	18	73	16	10	26				7	11	18	5		5				28		28
24	55	6	61	26	6	32	6		6	57	10	67	28	14	42				67	12	79	13		13				52		52
25	42	3	45	45	8	53	12		12	56	10	66	36	10	46				24	10	34	17		17				42		42
26	55	1	56	29	10	39	10		10	59	7	66	31	27	58				31	10	41	3		3				23		23
27	47	8	55	42	6	48	10		10	59	8	67	60	7	67				28	5	33	11		11				22		22
28	56	5	61	55	18	73	9		9	68	7	75	48	12	60				33	4	37	17		17				23		23
29	55	3	58	33	8	41	11		11	59	9	68	43	21	64				36	21	57	10		10				19		19
30	43	2	45	33	17	50	7		7	40	13	53	48	3	51				38	6	44	15		15				9		9
31	60	5	65	39	7	46	16		16	45	12	57	46	19	65				42	9	51	8		8				3		3
32	58	1	59	0	20	20	13		13	53	5	58	44	9	53				47	8	55	12		12				8		8
33	46		46	10		10	8		8	51	16	67	31	6	37				51	3	54	9		9				37		37
34	50		50	17		17	15		15	34		34	34	9	43				33	3	36	5		5				35		35
35	49		49	12		12	13		13	17		17	28	5	33				0	3	3	25		25				26		26
36				6		6	13		13				35	5	40				3		3	25		25				49		49
37				0		0	3		3				28	3	31							10		10				27		27
38							7		7				39	9	48							10		10				28		28
39							10		10				39	16	55							13		13				13		13
40							4		4				50	19	69							4		4				14		14
41													38	13	51							2		2				24		24
42													28	15	43							0		0				20		20
43													39	2	41													12		12
44													28	4	32													28		28
45													35	11	46													32		32
46													33	24	57													30		30
47													19	15	34													25		25
48													19	9	28													15		15
49													10	9	19													8		8
50													13		13													28		28
51																												24		24
52																												39		39
53																												27		27
54																												10		10
55																												10		10
56																												55		55
57																												36		36
58																												30		30
59																												37		37
60																												25		25
61																												19		19
62																												12		12
63																												7		7

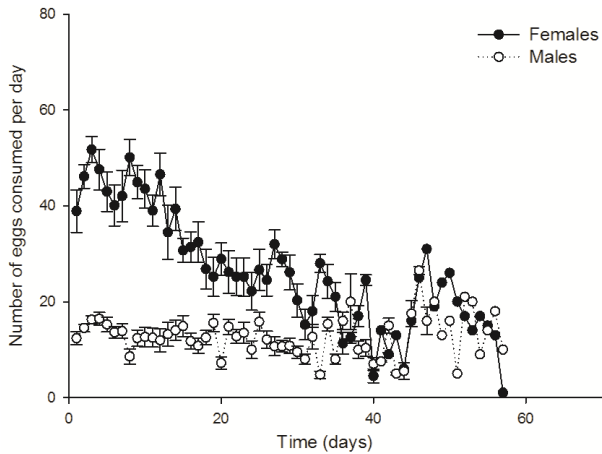| Replicates	f11	m11	c11	f12	m12	c12	f13	m13	c13	f14	m14	c14	f15	m15	c15	f16	m16	c16	f17	m17	c17	f18	m18	c18	f19	m19	c19	f20	m20	c20
Day 1	28	8	36	32	10	42	57	17	74	42	13	55	15	4	19	74	23	97	42	13	55	49	15	64	21	7	28	70	21	91
2	51	16	67	58	18	76	39	12	51	42	13	55	25	7	32	27	8	35	48	14	62	35	10	45	46	14	60	41	13	54
3	34	10	44	31	10	41	44	13	57	16	5	21	24	7	31	43	13	56	57	18	75	11	3	14	54	16	70	32	10	42
4	35	10	45	55	17	72	41	13	54	34	10	44	16		16	40	12	52	53	16	69	51	16	67	49	15	64	38	11	49
5	41	13	54	21	6	27	41	12	53	63		63	22		22	45	14	59	29	9	38	38	12	50	68	21	89	27	8	35
6	31	9	40	17	5	22	52	16	68	28		28	10		10	66	20	86	38	12	50	51	15	66	47	14	61	52	16	68
7	21	7	28	45	14	59	37	11	48	36		36	12		12	31	9	40	29	9	38	51	16	67	55	17	72	19	6	25
8	65	26	91	41	0	41	45	7	52	60		60	9		9	45	16	61	34	9	43	27	19	46	40	6	46	44	14	58
9	37	9	46	28	0	28	57	1	58	34		34	21		21	36	11	47	38	15	53	45	22	67	36	8	44	43	10	53
10	29	7	36	51	15	66	55		55	32		32	13		13	40	23	63	26	13	39	41	16	57	42	16	58	48	18	66
11	37	13	50	32	28	60	55		55	18		18	8		8	43	14	57	36	15	51	17	11	28	41	11	52			
12	41	5	46	38	2	40	50		50	20		20	10		10	24	8	32	34	16	50	32	8	40	24	5	29	35	7	42
13	19	9	28	31	14	45	47		47	1		1	6		6	21	15	36	48	7	55	44	10	54	24	15	39	64	6	70
14	4	14	18	22	12	34	53		53				7		7	2	19	21	46	16	62	44	9	53	7	10	17	35	10	45
15	21	10	31	34	11	45	51		51	6		6	5		5	45	21	66	36	9	45	32	11	43	0	5	5	29	9	38
16	36	0	36	39	15	54	15		15	5		5				45	3	48	38	15	53	24	19	43	11		11	30	10	40
17	47	0	47	45	12	57	16		16	13		13	16	13	29	49	0	49	44	14	58	17		17				31	20	51
18	20	17	37	40	7	47	51		51	8		8				16	14	30	45	14	59	0	11	11	9		9	14	17	31
19	39	17	56	5	13	18	42		42	12		12				20	16	36	29	16	45	6		6	15		15	48	8	56
20	38	11	49	52	5	57	24		24				4		4	25	28	53	20	18	38	6		6	12		12	42	13	55
21	41	10	51	53	15	68	3		3				0		0	15		15	44	10	54	17		17	15		15	28	14	42
22	54	7	61	42	19	61	0		0				6		6	15		15	44	11	55	12		12	9		9	22	26	48
23	48	10	58							6		6	0		0	16		16	33	9	42	8		8	9		9	28	12	40
24	54	17	71													11		11	54	6	60	18		18	2		2	23	10	33
25	48	13	61													15		15	38	17	55	6		6	4		4	12		12
26	26	14	40													6		6	21	7	28	3		3	3		3	8		8
27	9	11	20													4		4	18	9	27	2		2	5		5	2		2
28	11	13	24													5		5	14	17	31	2		2	2		2	4		4
29	16	8	24													24		24	4	9	13	25		25	25		25	17		17
30	9	4	13													28		28	30	22	52	23		23	11		11	23		23
31													6		6	4		4	38	11	49	21		21	6		6	14		14
32										24		24	22		22	5		5	20	11	31	22		22	22		22	15		15
33													22		22	5		5	29	5	34	24		24	29		29	24		24
34																2		2	15		15	17		17	15		15	14		14
35																2		2	18		18	21		21	16		16	16		16
36																13		13	11		11	12		12	21		21	16		16
37																13		13	14		14	5		5	14		14	14		14
38																			7		7	2		2	11		11	12		12
39																			22		22	0		0	10		10	10		10
40																			25		25							4		4
41																			15		15									
42																			5		5									

Figure 1. Average daily number of eggs eaten per male and female (± SE) adult of *C. infumatus* at 24 ± 1 °C, RH 70 ± 10% and 12-h photophase.
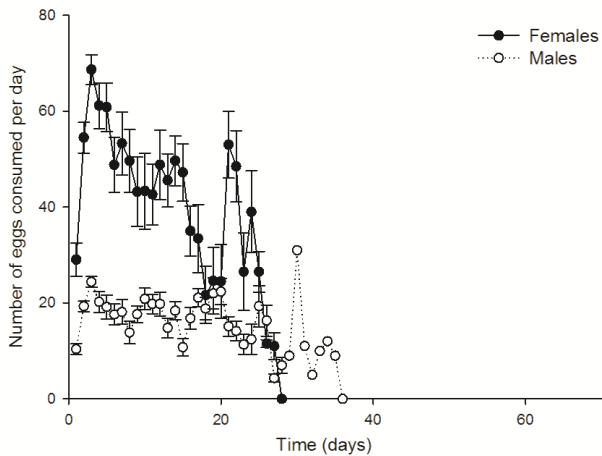

Figure 2. Average daily number of eggs eaten per male and female (± SE) adult of *E. varians* at 24 ± 1 °C, RH 70 ± 10% and 12-h photophase.
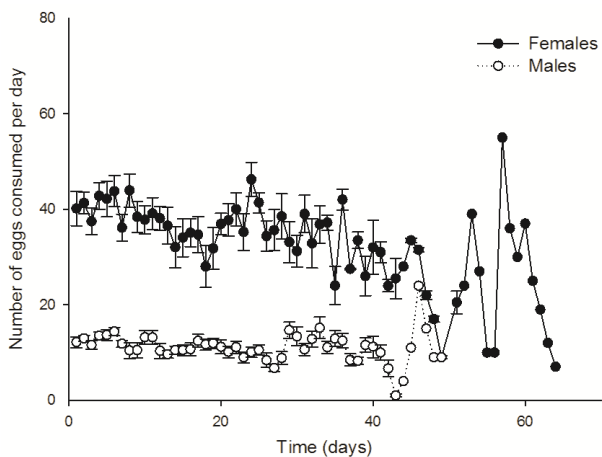

Figure 3. Average daily number of eggs eaten per male and female (± SE) of *M. basicornis* at 24 ± 1 °C, RH 70 ± 10% and 12-h photophase.

Table 2. Summary of data for total number of eggs eaten during adult life and number of eggs eaten per day for each sex of *C. infumatus*, *E. varians* and *M. basicornis*, calculated from life tables (table 1) that were constructed over the entire adult life of the predators (standard errors in parentheses; and in each case, n = 20).

Species/sex	Total # eggs	Eggs/day
C. infumatus male	336.95 (± 41.52)	13.34 (± 0.63)
C. infumatus female	844.65 (± 77.31)	38.99 (± 2.25)
E. varians male	313.45 (± 39.93)	17.30 (± 0.72)
E. varians female	668.20 (± 72.98)	49.01 (± 2.30)
M. basicornis male	339.20 (± 38.89)	11.19 (± 0.39)
M. basicornis female	934.30 (± 127.40)	35.38 (± 1.69)

negative trend was observed (table 4), indicating that predation rates tended to decrease with age of the predators. However, the variation was large, and the proportion of explained variance was always relatively low (low r², see table 4). Trends appeared to be stronger for females than for males, although this was not statistically tested.

Survival analysis

The Kaplan-Meier survivor plots are shown in figure 4. For these curves, the Log-rank test gave an overall significant difference (P < 0.0001). We fitted both an exponential model and a Weibull model to the data. The Weibull model fitted by far the best (AIC Weibull = 946.59; AIC exponential = 987.67). The males and females do not show a different survival, but males and females of *E. varians* lived significantly shorter than the other two species (table 5). The shape parameter *k* is larger than one, implying that the mortality rate increases in time.

Discussion

Longevity

Lifespans including fecundity and predation data have rarely been determined for mirid predators of *T. absoluta*. Mollá *et al.* (2014) recorded the life-table parameters of *Macrolophus pygmaeus* Rambur and *Nesidiocorus tenuis* (Reuter) (Hemiptera Miridae) when fed on *T. absoluta* eggs on tomato at 25 ± 1 °C, RH 60 ± 5%, and 16:8h L:D, and found adult lifespans of respectively 29.5 ± 2.5 (S.E) and 18.3 ± 1.6 (S.E.) (n = 25) days. Silva *et al.* (2016b) recently published data about the lifespans of the three Neotropical mirids we also studied, and which were determined under similar temperature, humidity and photophase conditions on the same tomato cultivar. For females and males of *E. varians* they found considerably longer lifespans than we did in the current experiment. The pattern of survival for males of *M. basicornis* is quite different in both experiments: in our experiment the males start to die earlier, but in the 2016 experiment all males had died before 40 days, while in our experiment the oldest male died at 49 days of age. The patterns for males and females of

Table 3. Contribution of the fixed factors 'species' and 'sex' to variation found in each of two response variables, measured on males and females of *C. infumatus*, *E. varians* and *M. basicornis*.

	Total # eggs		Eggs/day	
	F	p	F	p
Species	2.07	0.13	21.74	<0.001
Sex	65.70	<0.001	467.90	<0.001
Interaction	1.37	0.26	3.36	0.04
Overall model	14.52	<0.001	103.62	<0.001
Adj. R^2	0.36		0.81	
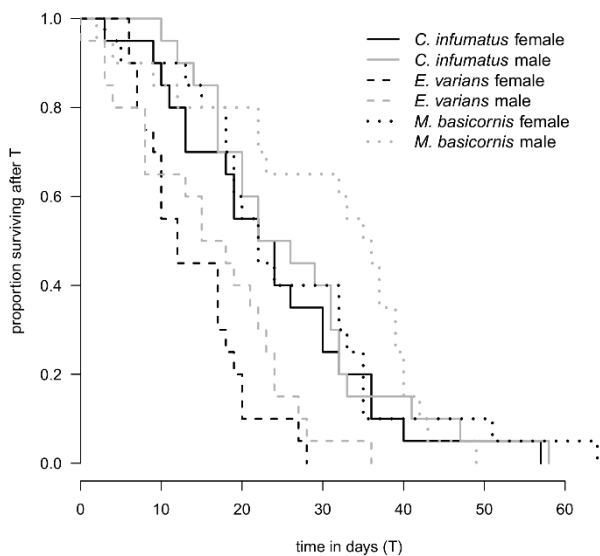
Figure 4. Kaplan-Meier survivor plots for males and females of *C. infumatus*, *E. varians* and *M. basicornis* on tomato at 24 ± 1 °C, 70 ± 10% RH and 12-h photophase.

Table 4. Weighted linear least square regression analyses of egg predation over time, for each sex separately of *C. infumatus*, *E. varians* and *M. basicornis*.

Species/sex	F	d.f.	significance	r^2
C. infumatus female	142.47	472	<0.001	0.23
C. infumatus male	7.91	527	0.005	0.015
E. varians female	38.97	279	<0.001	0.12
E. varians male	10.18	347	0.002	0.03
M. basicornis female	46.93	510	<0.001	0.08
M. basicornis male	0.37	594	NS	0.00

Table 5. Effect of the fixed factors 'species' and 'sex' on the survival of *C. infumatus*, *E. varians* and *M. basicornis*. The Weibull model resulted in a better fit than the exponential model. The baseline is the group of *C. infumatus* females. Shape parameter *k* is estimated as 1.75 and scale parameter λ as 25.48 days.

Species	β	effect exp (β)	χ^2 d.f. = 3	P
E. varians	0.498	1.645	15.21	0.002
M. basicornis	−0.107	0.900	0.70	0.87
Sex male	−0.130	0.878	1.55	0.67

Figure 5. A box and whiskers plot of the time to death for females and males of *C. infumatus*, *E. varians* and *M. basicornis*. The bold horizontal lines represent the median times, whereas the box shows the interquartile range (IQR) which is defined as the difference between the first quartile (Q1) or 25% point, and the third quartile (Q3) or 75% point. Fifty percent of the observations are in the interquartile range, while 25% of the observations are outside the box at either side. The white boxes are from our 2018 experiment and the grey boxes from the experiment by Silva *et al.* (2016).

Table 6. Adult longevity (± SE) found by Silva *et al.* (2016b) and in the current experiment for *C. infumatus*, *E. varians* and *M. basicornis*.

Species/sex	Longevity ± SE (n=30) Silva *et al.*, 2016b	Longevity ± SE (n=20) this paper
C. infumatus male	24.3 (± 0.91)	26.55 (± 2.72)
C. infumatus female	28.4 (± 0.66)	23.55 (± 2.87)
E. varians male	26.1 (± 0.93)	16.95 (± 2.01)
E. varians female	32.2 (± 0.42)	13.95 (± 1.50)
M. basicornis male	29.5 (± 0.67)	29.75 (± 3.11)
M. basicornis female	32.1 (± 0.52)	25.60 (± 3.23)

C. infumatus and for females of *M. basicornis* were not significantly different between the 2016 and 2018 experiments (table 6, figures 4 and 5).

We identified several differences in the experimental set-up of Silva *et al.* (2016b) and ours, which might explain (part of) the dissimilarities. Silva *et al.* (2016b) kept individual adults in large glass jars (1.7 L) with a tomato seedling with several leaves, and leaves on which adults had oviposited were replaced every three days. Instead, we used single tomato leaflets in a small

Petri dish (9 cm diameter) and replaced leaves daily. The much smaller space and the more frequent disturbance may have negatively influenced longevity, and, thus, also predation. Shorter longevities found by us may also partly be explained by the fact that we offered leaf discs, while Silva *et al.* (2016b) used whole seedlings, which provided the zoophytophagous mirids with better opportunities to make use of their phytophagous behaviour by feeding on the stems and petioles.

Based on the differences in female lifespan, we conclude that our estimates of total female lifetime predation are too low and might actually have been from 20% to up to 100% (*E. varians*) higher when adults would have been offered larger experimental containers, larger plants and has been disturbed less frequently. *E. varians* females and males showed the largest reduction in longevity in the small Petri dishes. We have repeatedly observed that this species is the most active of the three mirids in rearing cages and flies away from release containers much faster than the other species, and being confined to small Petri dishes might have negatively influenced this species stronger than the other two.

Lifetime predation

To our knowledge, this is the first time that total predation of *T. absoluta* eggs by males and females of mirids was determined during their entire adult lifespan. Mollá *et al.* (2014) reported total nymphal predation of *T. absoluta* eggs by two European mirids, and Mollá *et al.* (2014) and Abbas *et al.* (2014) presented data on nymphal predation of *E. kuehniella* eggs by three European mirids. Recently, we published total nymphal egg predation for the three Neotropical mirids: *C. infumatus*, *E. varians* and *M. basicornis* nymphs ate on average 315, 393 and 331 *T. absoluta* eggs, respectively (van Lenteren *et al.*, 2017). These numbers are twice as high as found for nymphal predation of *T. absoluta* eggs by *N. tenuis* and *M. pygmaeus* (Mollá *et al.*, 2014) and also higher than nymphal predation of *E. kuehniella* eggs by *Dicyphus maroccanus* Wagner (Hemiptera Miridae) (Abbas *et al.*, 2014).

We know of only one report presenting daily adult predation, but only for a period of 14 days and for one of the three mirids we studied (Smit, 2015): she found that *M. basicornis* consumed on average 563 eggs during 14 days, resulting in a predation rate of 40 eggs/day/adult. We found an average of 38.1 eggs/female/day, which is similar to what she found. There are literature data about predation of *T. absoluta* eggs during one day by mirid adults (Urbaneja *et al.*, 2009; Bueno *et al.*, 2013; van Lenteren *et al.*, 2016), but these are of limited value because of short-term measurements for one day only. Further, due to a period of starvation before the test, such tests tend to overestimate adult predation. For example, van Lenteren *et al.* (2016) found that *C. infumatus* consumed an average of 51.0 eggs, *E. varians* 91.1 eggs, and *M. basicornis* 100.8 eggs during a 24 hr predation period and after a starvation period of 24 hr. These predation rates are 30 to 250% higher than found for average daily predation rates during the whole adult lifespan in this experiment. The on average lower predation rates we found are not due to a strong decrease in daily predation over time, as the linear regression tests only showed a marginally significant trend (table 4), where the factor "time" explains only a very limited proportion of the variation in daily egg predation rates. Our conclusion is that one needs to determine predation rates during the lifespan of nymphs and adults in order to obtain reliable information about the predation capacity of a predator and to prevent overestimation.

Recently a lot of information became available about mirid predators attacking *T. absoluta* (e.g. Zappalà *et al.*, 2013). It has become clear that these generalist predators can play an important role in biological control and IPM programmes to control various pests on vegetables (e.g. Urbaneja *et al.*, 2012; van Lenteren *et al.*, 2018a). However, it is no exception to read in many of the articles cited in the three above mentioned papers, that researchers propose a certain natural enemy as a good candidate for biological control based on measuring only one or a few of its characteristics. It would be much better though, if we would have an aggregate parameter to compare potential efficacy of natural enemies, like the pest kill rate as used by Tommasini *et al.* (2004). For calculation of the pest kill rate, predation data for all developmental stages are needed, as well as data on developmental times, survival rates, sex ratios and adult lifespan. Our current paper provides lifetime predation data for adults of three Neotropical mirids. Together with the data on developmental time, survival and predation rates of nymphs (van Lenteren *et al.*, 2017; Bueno *et al.*, 2018), and data on egg development and survival (Silva *et al.*, 2016b, Bueno *et al.*, 2018), we will be able to calculate pest kill rates of the three mirids as well as the kill rate of a parasitoid (*Trichogramma pretiosum* Riley) used for control of *T. absoluta*, after having adapted the kill rate model used by Tommasini *et al.* (2004).

Acknowledgements

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