

Functional Response of Two Coccinellid Predators, *Scymnus levaillanti* and *Cycloneda sanguinea*, to the Cotton Aphid, *Aphis gossypii*

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Received: 30.11.2004

Abstract: Functional responses of 2 female coccinellid predators, *Scymnus levaillanti* and *Cycloneda sanguinea*, to the cotton aphid, *Aphis gossypii*, at various temperatures were studied under laboratory conditions. Both coccinellid species showed different functional responses to the cotton aphid. The larger species, *C. sanguinea*, was seen to eat more aphids than the smaller species, *S. levaillanti*, at each temperature, due to its greater voracity. The female adults of both coccinellid species feed maximally during the first 3 h and therefore, the increase in fresh weight gain and number of aphids killed by both coccinellid species are much higher during the first 3 h at each temperature than those during the following 3 h intervals. The consumption of cotton aphids by both coccinellid species had a type II functional response at each temperature. The parameters estimated from the type II functional response model suggest that *C. sanguinea* can be more effective at suppressing cotton aphid populations than *S. levaillanti* when the cotton aphid populations are large. This is because they have less time to process the cotton aphids and are more efficient searchers, requiring more cotton aphids to reach satiation than *S. levaillanti*.

Key Words: Coccinellid, *Scymnus levaillanti*, *Cycloneda sanguinea*, functional response, aphid density, handling time, attack constant

İki Avcı Coccinellid Türü, *Scymnus levaillanti* ve *Cycloneda sanguinea*'nin Pamuk Yaprakbiti, *Aphis gossypii*'ye Karşı İşlevsel Tepkisi

Özet: Avcı iki coccinellid türü, *Scymnus levaillanti* ve *Cycloneda sanguinea*'nin pamuk yaprakbiti, *Aphis gossypii*'ye karşı farklı sıcaklıklardaki işlevsel tepkileri laboratuvar koşullarında çalışılmıştır. Her iki coccinellid türü de farklı işlevsel tepki göstermiştir. Daha büyük tür olan, *C. sanguinea*'nin, daha küçük tür olan *S. levaillanti*'ye göre her sıcaklıkta daha fazla yaprakbiti tükettiği görülmüştür. Her iki coccinellid türünün ergin dişileri en fazla ilk üç saatlik zaman diliminde beslenmişlerdir ve bundan dolayı, ilk üç saatlik dilimdeki vücut ağırlığı artışı ve her iki coccinellid türü tarafından tüketilen yaprakbiti sayısı her sıcaklıkta ilk üç saatten sonraki zaman diliminden daha fazla bulunmuştur. Her iki coccinellid türünün pamuk yaprakbiti tüketimi, her sıcaklıkta tip II işlevsel tepki göstermiştir. Tip II işlevsel tepki modelinden elde edilen parametreler, *C. sanguinea*'nin pamuk yaprakbitini *S. levaillanti*'ye göre daha kısa sürede tükettiğini ve avını daha etkin aramadığını ve dolayısıyla doyuma ulaşması için daha fazla yaprakbitine gereksinim duyduğunu göstermiştir. Bu yüzden pamuk yaprakbiti popülasyonunun yüksek olduğu durumlarda, *C. sanguinea*'nin *S. levaillanti*'ye göre pamuk yaprakbiti popülasyonunu baskı altına almada daha başarılı olabileceği görülmüştür.

Anahtar Sözcükler: Coccinellid, *Scymnus levaillanti*, *Cycloneda sanguinea*, işlevsel tepki, yaprakbiti yoğunluğu, avı tüketme süresi, avı arama oranı

Introduction

The cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), is a cosmopolitan species widely distributed in tropical, subtropical and warm temperate regions. It is a worldwide pest of many plant species including cotton, cucurbits (melon, courgette, cucumber), citrus, coffee, vegetables (eggplant, okra, sweet pepper etc.) and ornamental plants (*Lantana*, *Hibiscus*, *Chrysanthemum*)

(Blackman and Eastop, 1984). *Scymnus levaillanti* Mulsant is mainly an aphidophagous coccinellid species and is among the dominant coccinellid predators of *A. gossypii* on cotton in Turkey (Kışmir, 1983). Based on information on the biology of *S. levaillanti* and its feeding capacity, Uygun and Atlihan (2000) reported that *S. levaillanti* may act as an important control agent. *Cycloneda sanguinea* (L.) is primarily an aphidophagous

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coccinellid species and is most common in temperate areas of Central and South America (Vandenberg and Gordon, 1988). Little information is available on the response of these coccinellid species to the changes in the density of *A. gossypii* and therefore it is not known whether they may be expected to prevent or suppress population increases of *A. gossypii*.

Predators react to the density of prey in several ways, which were first described and defined by Solomon (1949) and then analysed in a complex manner by Holling (1959, 1965). The responses of a predator to changes in prey density can be divided into a functional response, which is the change in the number of prey consumed per predator in response to changing prey density, and a numerical response, the change in predator density resulting from a change in prey density (Solomon, 1949). When the number of prey killed is plotted against the number of prey available, a continuum of patterns may emerge from which ecologists delimit 3 types of functional response (Holling, 1966; Trexler et al., 1988). Several other types of functional response have been reported: type IV (Luck, 1985) and type V (Sabelis, 1992). Coccinellids show a type II functional response, as was reported, for example, for larva of *Harmonia axyridis* (Pallas) (Mogi, 1969), *Propylea japonica* L. (Kawauchi, 1991), *S. levaillanti* (Uygun and Atlihan, 2000), *Stethorus punctillum* Weise (Yi?it and Uygun, 1986) and *Coccinella septempunctata* L. (Sinha et al., 1982), and for adult *Cheilomenes sulphurea* (Olivier) (Hodek et al., 1984) and *Cheilomenes lunata* (Fabricius) (Ofuya and Akingbohunge, 1988). *C. septempunctata* larvae preying on small cabbage aphids (*Brevicoryne brassicae* (L.)) were reported to show a type III response (Hassell et al., 1977).

A functional response is usually measured to provide insights into the suitability of a predator as a biological control agent. The type of functional response, that is the shape of the relationship of the number prey eaten versus prey available, influences the dynamics of the predator-prey population and may contribute to stability of predator-prey systems (Hassell, 1978; Taylor, 1980). Thus, the objectives of this study were to determine the effect of aphid density on the number of aphids killed by the female adults of *S. levaillanti* and *C. sanguinea* at various temperatures, to determine the type of functional response, and to estimate and compare the parameters of the functional response of these 2 coccinellid predators.

Materials and Methods

Test insects and experimental arena

A culture of insect materials, both aphid and coccinellid predators, was established in controlled temperature rooms. The cotton aphids, *A. gossypii*, and the coccinellid predator, *S. levaillanti*, were collected from the Haciali Cotton Research Centre near Adana in Turkey while the coccinellid predator, *C. sanguinea*, was collected from fields near Merida in Mexico by the second author. Cotton (*Gossypium hirsutum* L.) and okra (*Hibiscus esculentus* L.) plants grown in a glasshouse were used as host plants for production of the cotton aphids. Aphid and predator cultures were maintained in a growth room at 25 ± 1 °C, $55 \pm 10\%$ r.h., and a photoperiod of 16L:8D.

The studies were conducted at 3 constant temperatures, namely 20, 25 and 30 ± 1 °C with a 16L:8D photoperiod, in incubator cabinets with $60 \pm 5\%$ r.h. maintained using a saturated salt solution of magnesium nitrate (MgNO_3). Female adults were taken from the stock culture, starved for 24 h at 25 °C in the incubator cabinets in order to standardise their appetite, and then weighed using a micro-balance (accurate to 0.001 mg) to record their initial fresh body weights prior to being introduced into feeding arenas. Thereafter, they were introduced individually into 9 cm diameter petridishes (approximately 64 cm²) together with 3, 6, 10, 20, 40, 80, 120 and 240 and 20, 40, 80, 120, 240, 480 and 960 aphid densities for *S. levaillanti* and *C. sanguinea* respectively on excised cotton leaves stuck to agar medium. Medium size aphids were selected (mean weight \pm standard error: 0.043 mg \pm 0.0014). One of every 2 petridishes was placed in a large transparent box (27 x 16 x 10 cm) with a saturated salt solution of MgNO_3 in a small cup. Female adults of *S. levaillanti* and *C. sanguinea* were randomly assigned to 1 of 8 and 7 aphid density treatments respectively. At each aphid density, 5 to 9 and 5 to 8 replicates were used for *S. levaillanti* and *C. sanguinea* respectively (Tables 1 and 2). After 24 h, the number of aphids killed by the female adults were recorded by counting the aphids remaining in each dish.

Experimental procedure for the functional response of *S. levaillanti* and *C. sanguinea*

At aphid densities of 240 and 480 for *S. levaillanti* and *C. sanguinea* respectively, female adults were weighed using a micro-balance (accurate to 0.001 mg) to

Table 1. Parameter estimates (\pm SE) for logistic regressions of the proportion of prey killed against the number of prey offered (No) for the female adults of *Scymnus levallanti* and *Cycloneda sanguinea* for 24 h.

Parameters	20 °C		25 °C		30 °C	
	<i>S. levallanti</i>	<i>C. sanguinea</i>	<i>S. levallanti</i>	<i>C. sanguinea</i>	<i>S. levallanti</i>	<i>C. sanguinea</i>
Intercept	0.86*** (0.08)	1.05*** (0.05)	0.98*** (0.06)	1.0*** (0.008)	1.05*** (0.03)	1.0*** (0.005)
Linear	-0.025* (0.006)	-0.0016 (0.0008)	-0.011* (0.004)	0.00008* (0.0001)	-0.012** (0.002)	-0.0002* (0.00007)
Quadratic	0.00023* (0.00007)	-0.00000016 (0.000002)	0.000055 (0.00005)	-0.000002* (0.0000004)	0.00006 (0.00003)	0.0000007* (0.0000002)
Cubic	-0.0000006* (0.0000002)	0.0000000009 (0.0)	-0.000000096 (0.0000002)	0.000000001* (0.0)	-0.00000009 (0.00000008)	-0.00000001** (0.0)
r ²	0.93	0.99	0.96	0.99	0.99	0.99
F and P Value	F = 17.4 d.f. = 3, 4 P < 0.01	F = 73.5 d.f. = 3, 3 P < 0.01	F = 33.5 d.f. = 3, 4 P < 0.01	F = 1196.7 d.f. = 3, 3 P < 0.01	F = 146.8 d.f. = 3, 4 P < 0.01	F = 2326.1 d.f. = 3, 3 P < 0.01

Significant coefficients are indicated by asterisks: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Table 2. Estimated type II response parameters for the female adults of *Scymnus levallanti* and *Cycloneda sanguinea* for 24 h at various temperatures.

Predator Species	20 °C			25 °C			30 °C		
	a \pm SE (95% C.I.) ³	Th \pm SEr ² (95% C.I.) ³	0.987	a \pm SE (95% C.I.) ³	Th \pm SEr ² (95% C.I.) ³	0.994	a \pm SE (95% C.I.) ³	Th \pm SEr ² (95% C.I.) ³	0.998
<i>S. levallanti</i> Disc Eq. ¹	0.034 \pm 0.007 (0.016-0.052)	1.75 \pm 0.13 (1.44-2.07)	0.987	0.058 \pm 0.0075 (0.039-0.076)	0.62 \pm 0.032 (0.54-0.699)	0.994	0.063 \pm 0.007 (0.045-0.081)	0.602 \pm 0.023 (0.533-0.671)	0.995
<i>C. sanguinea</i> Disc Eq. ¹	0.071 \pm 0.016 (0.028-0.11)	0.12 \pm 0.012 (0.087-0.15)	0.984	0.058 \pm 0.0067 (0.041-0.075)	0.038 \pm 0.0037 (0.029-0.048)	0.994	0.059 \pm 0.009 (0.034-0.083)	0.025 \pm 0.0044 (0.014-0.036)	0.989
<i>S. levallanti</i> Ran. Pre. Eq. ²	0.044 \pm 0.014 (0.009-0.077)	1.78 \pm 0.15 (1.41-2.15)	0.983	0.13 \pm 0.021 (0.079-0.18)	0.69 \pm 0.021 (0.64-0.74)	0.998	0.16 \pm 0.022 (0.11-0.21)	0.67 \pm 0.015 (0.63-0.71)	0.998
<i>C. sanguinea</i> Ran. Pre. Eq. ²	0.27 \pm 0.13 (-0.067-0.62)	0.14 \pm 0.008 (0.12-0.16)	0.994	0.24 \pm 0.02 (0.19-0.29)	0.053 \pm 0.0008 (0.051-0.055)	0.999	0.69 \pm 0.054 (0.55-0.83)	0.043 \pm 0.0003 (0.042-0.043)	0.999

For both species, the type II functional response equations were: ¹ disc equation ($N_e = [aN_0T/(1 + aN_0T)]$) and ² random predator equation ($N_e = N_0[1 - \exp(-a(TN_e - T))]$). ³ 95% confidence interval. Time units are hours.

record their initial fresh body weights prior to being introduced into the feeding arenas. Thereafter, the petridishes were checked every 3 h after releasing the female adults into the Petri dishes for up to 24 h and the number of aphids killed and their weight gains were noted at 3 different temperatures, but the aphids killed were not replaced during the feeding time. The weight of

the eggs of *S. levallanti* and *C. sanguinea* were calculated to be 0.016 mg \pm 0.00042 and 0.17 mg \pm 0.0042 (mean \pm standard error) respectively by weighing 20 eggs for each species. The weights of eggs laid by the female adults were added to the fresh weight gain of female adults of both species.

Data processing and analysis

The numbers of aphids killed by *S. levaillanti* and *C. sanguinea* in 24 h at different aphid densities and temperatures were analysed separately using one-way analysis of variance (ANOVA) to test for significance between aphid density and temperature treatments. The means were separated using the LSD method at 1% level (SAS Institute, 1985). Trexler et al. (1988) showed that logistic regressions of proportion of prey killed (N_e , number of aphids killed, / N , number of aphids offered) against the number of prey offered (N) provided a more powerful and accurate means of distinguishing between type II or III functional responses compared to analysis of the typical functional response curve (i.e. N_e against N). Briefly, to determine the shape, a polynomial regression is fitted to observed proportions of prey killed against N , and the shape of this polynomial fit is determined. If the proportion killed initially increases with the number of prey, this is sufficient to identify a type III functional response. If, on the other hand, the proportion killed declines monotonically with the number of prey, this is sufficient to identify a type II functional response. Thus, logistic regressions of proportion of aphids killed against number of aphids offered were used in this way to determine the general shapes of the functional responses of the female adults of *S. levaillanti* and *C. sanguinea* at each temperature.

The most widely used description of a type II functional response of invertebrate predators to changes in prey density is the disc equation given by Holling (1959):

$$N_e = \frac{ATN_o}{1 + aTh} \quad (1)$$

where N_e is the number of prey attacked, N_o is initial prey density, a is the predator's rate of successful search, Th is the handling time per prey item and T is the length of time the predator and prey are exposed to one another. Another deterministic model of a type II functional response, having similar restrictive assumptions but allowing for exploitation, was developed concurrently by Royama (1971) and Rogers (1972). The model known as the 'random predator' equation:

$$N_e = N_o\{1 - \exp[a(ThN_e - T)]\} \quad (2)$$

where N_e is the number of prey attacked, N_o is initial prey density, a is the predator's rate of successful search, Th is the handling time per prey item and T is the length of time the predator and prey are exposed to one another.

For type III functional responses, the precise form of the model incorporating depletion depends on whether the attack constant (a) is a function of initial density (N_o) or current density (N) (Hassell et al., 1977; Hassell, 1978). The simplest form arises when attack rate (a) is a function of initial density, as in Equation 2:

$$N_e = N_o\{1 - \exp[(d + bN_o)(ThN_e - T)/(1 + cN_o)]\} \quad (3)$$

Once the type of functional response was determined, the number of aphids killed as a function of aphid density for each temperature was plotted, and an iterative non-linear least-squares regression (SAS Institute, 1985) was used to fit the disc equation and random predator equation to the means and to estimate the parameters for type II functional responses. However, a non-linear least-square regression was used to fit Hassell's equation (Equation 3) to the data for type III functional responses.

Results

The number of aphids killed by *S. levaillanti* increased significantly with increasing aphid density up to 120 aphids/64 cm² at 20 °C ($F_{7,39} = 26.5$, $P < 0.01$) and 25 °C ($F_{7,50} = 51.8$, $P < 0.01$), and 80 aphids/64 cm² at 30 °C ($F_{7,44} = 66.4$, $P < 0.01$). Thus, there was no significant difference between number of aphids killed at aphid density of 120 and 240 at 20 and 25 °C. It seems that temperature also had a significant effect on the number of aphids killed at each aphid density (Figure 1a). The number of aphids killed was significantly higher at 25 and 30 °C than at 20 °C at each aphid density (except at densities of 3 and 6), whilst there was no significant difference between the numbers of aphids killed at 25 and 30 °C.

The number of aphids killed by *C. sanguinea* increased significantly with increasing aphid density at 25 °C ($F_{6,33} = 89.3$, $P < 0.01$) and 30 °C ($F_{6,40} = 929$, $P < 0.01$) whilst it increased significantly with increasing aphid density up to 240 aphids/64 cm² at 20 °C ($F_{6,29} = 39.7$, $P < 0.01$). There was a significant difference in number

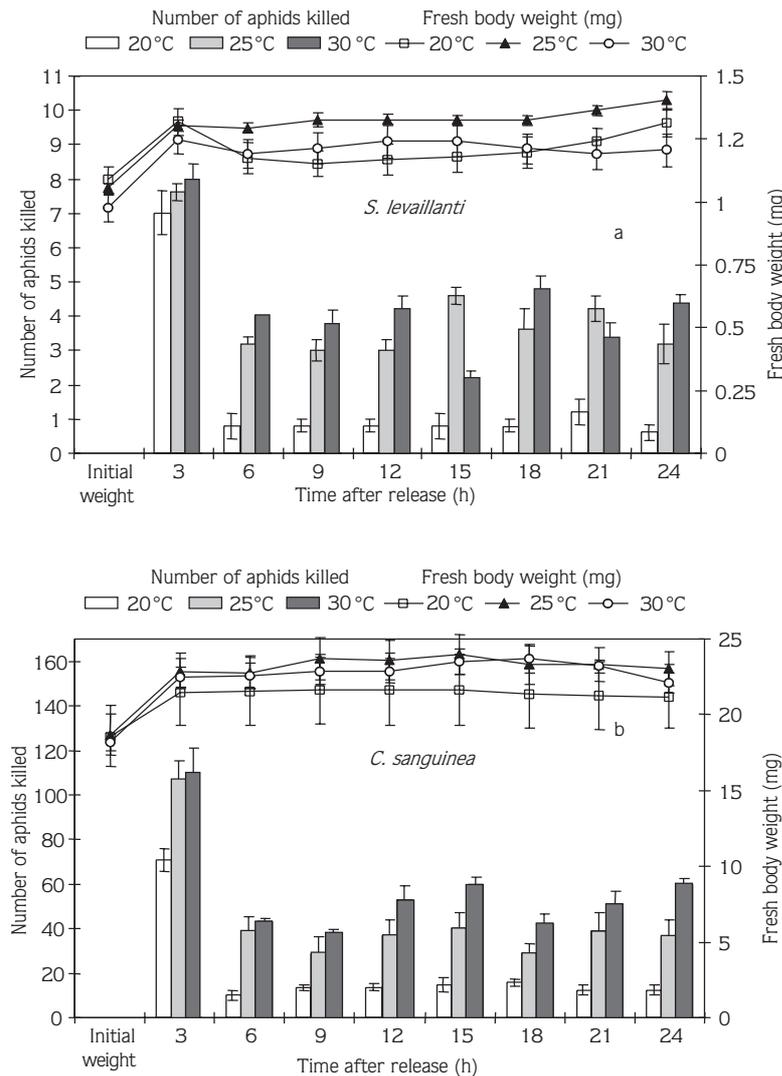


Figure 1. Changes in the fresh body weight and number of aphids killed by the female adults of (a) *Scymnus levallanti* and (b) *Cycloneda sanguinea* every 3 h after release at various temperatures. = standard error of fresh body weight and number of aphids killed. Five individuals as a replicate were used for both coccinellid species ($n = 5$). The bars indicate the mean number of aphids killed and the lines indicate the mean fresh body weight.

of aphids killed at the aphid densities at 25 (except first 3 densities of 20, 40, and 80) and 30 °C. The number of aphids killed was significantly higher at 25 °C and 30 °C than at 20 °C at each aphid density (except at 20 and 40), whilst there was significant difference between the number of aphids killed at 25 and 30 °C at aphid density of 480 and 960 (Figure 1b). At the lowest aphid densities (20 and 40 for *C. sanguinea*, and 3 for *S. levallanti*), all predators killed all the aphids offered. As the aphid density increased, predators showed more variation in

the number of aphids killed, as shown by the greater standard errors (Figure 1a and 1b).

The increase in fresh weight gain and number of aphids killed by both coccinellid species were much higher during the first 3 h at each temperature than those during the following 3 h intervals (Figure 1a and 1b). The fresh body weights of both coccinellid species remained relatively constant except for some small fluctuations during the following 3 h intervals. The number of aphids

killed by *S. levaillanti* also remained relatively constant, varying between 1 and 1.5 aphids/3 h at 20 °C, 2.5 and 4 aphids/3 h at 25 °C, and 2.5 and 4.5 aphids/3 h at 30 °C, whilst it was between 10 and 15 aphids/3 h at 20 °C, 25 and 35 aphids/3 h at 25 °C, and 37 and 50 aphids/3 h at 30 °C for *C. sanguinea*.

Parameter estimates for logistic regressions of proportion of prey killed (Ne/No) against number of prey offered (No) for the female adults of *S. levaillanti* and *C. sanguinea* for 24 h are presented in Table 1. Type II functional responses are evidenced by an initial decrease in the proportion of prey eaten with increasing prey offered (Trexler et al., 1988; Juliano, 1993). For *S. levaillanti* at 20, 25 and 30 °C, the linear coefficient was significant and negative (Table 1), indicating monotonic decreases in proportion killed against the number of aphids offered. These results show a type II functional response for *S. levaillanti* at 3 temperatures. On the other hand, the best polynomial included significant quadratic and cubic terms for *S. levaillanti* only at 20 °C (Table 1).

For *C. sanguinea* at 25 °C, the best polynomial included significant linear, quadratic, and cubic terms, and, most importantly, the linear term was positive (Table 1). The resulting function shows clearly the initial increase in the proportion eaten against the number of aphids offered that is characteristic of a type III functional response. For *C. sanguinea* at 20 °C, the best polynomial included non-significant linear, quadratic, and cubic terms, but the linear term was negative (Table 1). The resulting function, although clearly non-linear, shows no evidence of an increase in the proportion killed against the number of aphids offered and thus is consistent with a type II functional response. For *C. sanguinea* at 30 °C, the best polynomial included significant linear, quadratic, and cubic terms, and the linear term was negative (Table 1), indicating monotonic decreases in the proportion killed against the number of aphids offered. This result indicates a type II functional response. Thus, logistic regression analysis of both coccinellid species at 3 temperatures indicated that only *C. sanguinea* at 25 °C was consistent with a type III response.

At each temperature *S. levaillanti* yielded significant non-linear regressions for both the disc and the random predator equation. The *a* (attack constant) estimated from both disc equation and random predator equation increased with increasing temperature, whilst the *Th* (handling time) decreased with increasing temperature

(Table 2). They had a higher *Th* and a lower *a* at low temperature (20 °C) than at high temperatures (25 and 30 °C). Since logistic regression analysis showed that *C. sanguinea* had a different type of functional response at different temperatures, we simply fit a type III model (Hassell's equations) incorporating prey depletion at 25 °C and a type II model (both disc equation and random predator equation) at 20, 25, and 30 °C. Thereafter, the parameters were estimated for both type II and type III models.

The *Th* (handling time) from both the type II disc equation and the random predator equation decreased with increasing temperature (Table 2), whereas the *a* (attack constant) estimated from both type II models increased with increasing temperature from 25 to 30 °C whilst it decreased with increasing temperature from 20 to 25 °C for both type II models. They had a higher *Th* and a estimated from the disc equation at low temperature (20 °C) than at high temperatures (25 and 30 °C), but they had a lower *a* estimated from the random predator equation at a low temperature (20 °C) than at a high temperature (30 °C).

The handling times (*Th*) estimated from the random predator equation at each temperature were slightly higher for both coccinellid species than those estimated from the disc equation, whilst the random predator equation gave much higher attack constants (*a*) than the disc equation (Table 2). *Cycloneda sanguinea* had much shorter handling times (*Th*) estimated from both type II models at each temperature than *S. levaillanti*, but *C. sanguinea* had higher attack constants estimated from both type II models than *S. levaillanti* (except at 20 °C). For *C. sanguinea* at 25 °C, several alternative type III models (Juliano, 1993) were tested wherein the attack constant is an increasing function of the number of prey. The only model that yielded a significant regression was one where the attack constant = $d + bNo$ ($b = 0.0003 \pm 0.0001$, $d = 0.1602 \pm 0.039$ and $Th = 0.056 \pm 0.0009$). The resulting graphic presentation (Figure 2b), although incorporating a positive relationship between the attack constant and the number of aphids offered, shows little evidence of the sigmoid shape characteristic of type III functional responses. It seems that they had a rather weak form of a type III functional response. The type III functional response model yielded a lower residual sum of squares (33.62), indicating a better fit, than did the type II functional response model (65.44).

The graphic presentation of observed and predicted values fitted to both type II models (Figure 2a and 2b) indicated that the number of aphids killed by both coccinellid species increased more rapidly with an increasing number of aphids at the higher temperatures (25 and 30 °C) than at the lower temperature (20 °C). They also suggested that the asymptotic numbers of prey killed by both coccinellid species at high aphid numbers were greater at the higher temperatures (25 and 30 °C) than at the lower temperature (20 °C).

Discussion

The functional response of a natural enemy offers a good conceptual framework for understanding the action of agents in inundative releases (Waage and Greathead, 1988). It seems that aphid density and temperature play a very important role in the number of aphids killed by both coccinellid species in which coccinellid species showed different functional responses. The larger species, *C. sanguinea*, was shown to eat more aphids than the smaller species, *S. levallanti*, at each temperature,

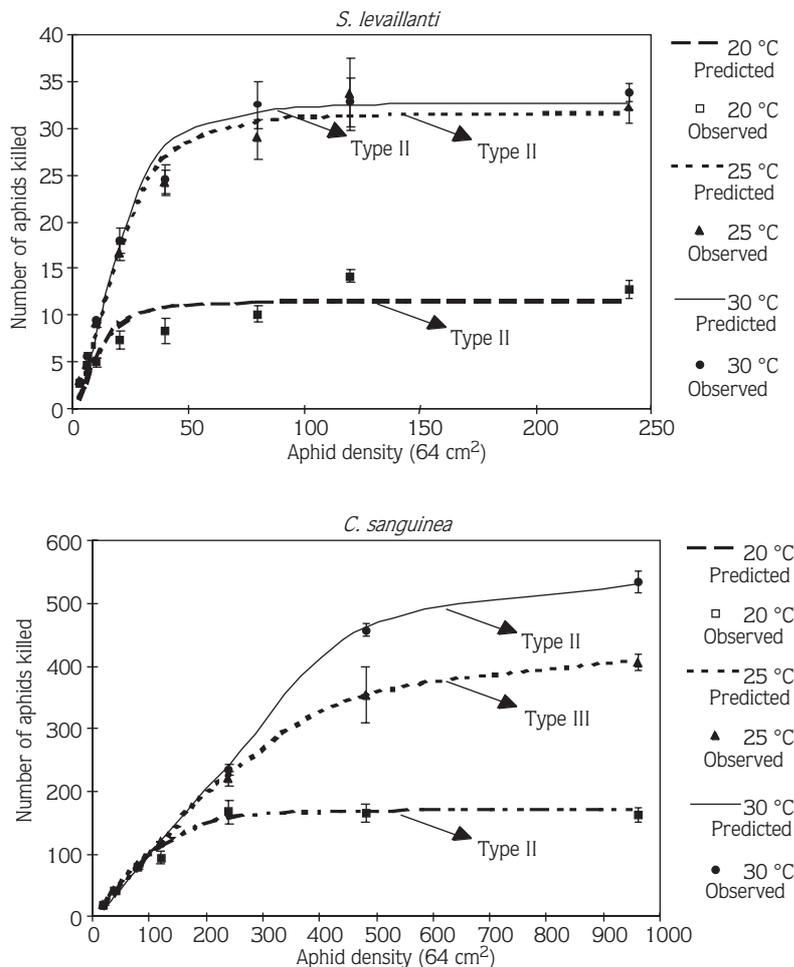


Figure 1. Changes in the fresh body weight and number of aphids killed by the female adults of (a) *Scymnus levallanti* and (b) *Cycloneda sanguinea* every 3 h after release at various temperatures. = standard error of fresh body weight and number of aphids killed. Five individuals as a replicate were used for both coccinellid species (n = 5). The bars indicate the mean number of aphids killed and the lines indicate the mean fresh body weight.

apparently due to its greater voracity. Morales and Burandt (1985) reported that the number of the brown citrus aphid, *Toxoptera citricida*, killed by the female of *C. sanguinea* increased with greater prey density at 25 °C and 42.6 brown citrus aphids were killed at the highest density (aphid density of 50). This result is much lower than that found in this study for *C. sanguinea*. This could be due to differences in the aphid species used in the experiment since the brown citrus aphid is a much bigger species than the cotton aphid used in this study.

The female adults of both coccinellid species feed maximally during the first 3 h and therefore the increase in fresh weight gain and number of aphids killed by both coccinellid species are much higher during the first 3 h at each temperature than those during the following 3 h intervals. It seems that previously starved female adults would allocate most of the aphids eaten during the first 3 h to cover the weight lost during the starvation period, whereas female adults being satiated after the first 3 h would consume a certain number of aphids only to oviposit the eggs and to cover the cost of metabolism. Similarly, Shukla et al. (1990) reported that the rate of prey consumption of *C. septempunctata* on *Lipaphis erysimi* Kalt. increased significantly with an increase in predation period as well as in prey density, and more than 50% of consumed prey were devoured during the first 3 h, which shows that the predator feeds maximally during this period.

Coccinellids usually show a type II functional response, as was reported, for example, for larva of *H. axyridis*

(Mogi, 1969), and for adult *Cheilomenes sulphurea* (Hodek et al., 1984), *C. lunata* (Ofuya and Akingbohunge, 1988) and *Scymnus hoffmanni* (Ding-Xin, 1986). Similarly, in our study, consumption of the cotton aphids by both coccinellid species evoked a type II functional response at each temperature (except for *C. sanguinea* at 25 °C having type III). Since the parameters estimated from type II functional responses indicated that the female adult *C. sanguinea* had a significantly shorter handling time and lower search rate compared to *S. levaillanti*, they takes shorter time to process the food and are more efficient searchers, requiring more aphids to reach satiation than *S. levaillanti*. Therefore, *C. sanguinea* can be more effective at suppressing cotton aphids when their populations are large. Once the cotton aphid exceeds the relatively low level at which the female adults of *S. levaillanti* are satiated, they can't be effective against the aphids. The functional responses of predators tend to level off due to satiation, causing the maximum predation rate to settle at much lower values than expected from the predator's time budget for handling and searching (Sabelis, 1992). Therefore, this can limit the success of cotton aphid control by these coccinellid species.

Acknowledgements

I would like to express my sincere thanks to the Higher Educational Council of the Republic of Turkey and Kahramanmaraş Sütçü İmam University for their financial support of this study.

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