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Feeding and Foraging Behaviour in Two Coccinellid Predators: *Scymnus levaillanti* Muls. and *Cycloneda sanguinea* L.

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Abstract: Predatory behaviour, prey consumption, and foraging cycle of adults and larvae of *Scymnus levaillanti* Muls. and *Cycloneda sanguinea* L. (Coleoptera: Coccinellidae) were investigated using a video/computer recording and measurement system. Larvae of *S. levaillanti* spent more time in feeding activities compared to *C. sanguinea*. Adults of both *S. levaillanti* and *C. sanguinea* spent more time in non-feeding activities (digestion and cleaning) compared to their larvae whilst adults of *S. levaillanti* spent less time in non-feeding activities than those of *C. sanguinea*. Generally, larvae and adults of both coccinellid species spent most of their time in non-feeding activities. Although *S. levaillanti* exhibited more foraging cycles with shorter periods compared to *C. sanguinea*, *S. levaillanti* required less aphids to be satiated compared to *C. sanguinea*. These results indicated that feeding and foraging behaviour of these coccinellid species can have a great impact on their daily aphid consumption.

Key Words: *Scymnus levaillanti*, *Cycloneda sanguinea*, coccinellid, foraging cycle, digestive pause

İki Coccinellid Predatör, *Scymnus levaillanti* Muls. ve *Cycloneda sanguinea* L.'nın Beslenme ve Besin Arama Davranışı

Özet: *Scymnus levaillanti* Muls. ve *Cycloneda sanguinea* L. (Coleoptera: Coccinellidae) larvalarının ve erginlerinin avlanma davranışı, av tüketimi, ve av arama döngüsü video/bilgisayar kayıt ve analiz sistemi kullanılarak araştırılmıştır. *Scymnus levaillanti* larvaları beslenme aktivitelerinde *C. sanguinea*'nın larvalarına göre daha fazla süre harcamışlardır. *Scymnus levaillanti* erginleri beslenme dışı aktivitelerde (sindirim ve temizleme) *C. sanguinea* erginlerine göre daha az süre geçirirken, hem *C. sanguinea* hem de *S. levaillanti* erginleri beslenme dışı aktivitelerde larvalara göre daha fazla süre geçirmişlerdir. Genel olarak her iki coccinellid türünün ergin ve larvaları zamanlarının çoğunu beslenme dışı aktivitelerde geçirmişlerdir. Buna göre S. levaillanti, *C. sanguinea*'ya göre daha kısa aralıklarla daha fazla besin arama döngüsüne sahip olmasına rağmen, doymak için daha az yaprak bitine ihtiyaç duymuştur. Bu sonuçlar, bu coccinellid türlerinin beslenme ve besin arama davranışları bunların günlük olarak tüketeceği yaprakbiti sayısı üzerine önemli etkiye sahip olabileceğini göstermiştir.

Anahtar Sözcükler: *Scymnus levaillanti*, *Cycloneda sanguinea*, coccinellid, beslenme döngüsü, sindirim aralığı

Introduction

The imaginal life of an insect is a chain of several types of activities comprising food search and consumption, mate search and copulation, resting and grooming. The timing and sequence of these behaviours determine the patterns of energy and matter allocation, and the overall fitness of an individual. In addition, they affect predation rate and a predator's ability to control a given species of prey. Most of the predation models developed, such as Holling's model, is based on behavioural components of the predator-prey interaction (Holling, 1959). The predation process is characterized by 'attack cycles' (Holling, 1966) with a period of foraging and digestive pause associated with the capture of each prey. The duration of activities within an attack cycle is dependent on the level of hunger, determined by the content of the gut.

The foraging cycle of the satiation model developed by Mills (1982) allows for a number of prey items to be fed before satiation limits the time devoted to predator

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search. In addition, hunger is not considered as a component influencing the timing of events within a foraging cycle in this model. For example, with considering one attack cycle, it is referred to the period leading up to and including the attack on one prey. Initially, just after the previous prey is eaten, hunger is below the threshold level that causes the predator to search for or attack another prey. Once the predator becomes satiated after a series of prey captures that fill its gut to capacity, it enters a period of digestive pause dependent on the retention time of food in the gut and the hunger threshold. After a period of digestive pause, the hunger rises to this threshold, and the predator responds again to the presence of prey (Holling and Buckingham, 1976).

The total time available for predation consists of the time spent in feeding and non-feeding activities such as walking, cleaning, and resting. For predators in the field, non-predatory activities that are essential to their survival and reproduction may overlap with the time spent in digestive pause within the foraging cycles. The total time available for predation may then vary with prey density. When prey is smaller than the predator and at low prey density, there is no digestive pause, and non-feeding and feeding activities will compete for the time available. At the other extreme, when the prey is larger than the predator, or when small prey are abundant, the time spent in digestive pause may be sufficient to incorporate all non-feeding activities (Mills, 1982).

Several laboratory studies on evaluation of the potential of 2 coccinellid species, *Scymnus levaillanti* Mulsant and *Cycloneda sanguinea* (L.), for the biocontrol of cotton aphid, *Aphis gossypii* Glover, were reported by Isikber and Copland (2001), Bocia Junior et al. (2004), and Işıkber (2005). Isikber and Copland (2001) reported that the larger species, *C. sanguinea*, was more voracious at each temperature than the smaller species, *S. levaillanti*. In another study, the parameters estimated from the type II functional response model suggested 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* (Işıkber, 2005).

Although the effectiveness of coccinellids depends largely upon the voracity of a particular species, understanding predator foraging strategies is of primary importance to the development of successful biological control. In this study, feeding and foraging behaviour of 2 aphidophagous coccinellid species, *Scymnus levaillanti* and *Cycloneda sanguinea*, were evaluated in relation to aphid consumption under laboratory conditions. The duration and sequence of predatory activities and the relationship between the prey consumption and foraging cycle of adults and larvae of *S. levaillanti* and *C. sanguinea* were investigated.

Materials and Methods

Test Insects and Experimental Arena

Cultures of both aphids and coccinellids were established in a growth room at 25 ± 1 °C, with a LD 16:8 h photoperiod and 55 ± 10% RH. The cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae), and the coccinellid predator, *S. levaillanti* were collected from Hacıali Cotton Research Centre near Adana, Turkey while the coccinellid, *C. sanguine,* was collected from fields near Merida, Mexico. Third-fourth instar (medium size) cotton aphids were used as food for the coccinellids, *S. levaillanti* and *C. sanguinea*, during all experiments. Cotton aphids were reared on cotton (*Gossypium hirsutum* L.) grown in a glasshouse. Prior to each experiment, 2 weeks-old adults and 1 day-old larvae of both coccinellid species were starved for 24 h. Before each experiment, a single excised cotton leaf, stuck axial surface upwards on agar medium (8 g l^{-1}), was placed in plastic Petri-dishes (15 60 mm) and 240 third-fourth instar cotton aphids were transferred onto the excised leaf and allowed to settle and start feeding for 6 h. To determine their fresh weight, fifty third-fourth instar cotton aphids were weighed using a microbalance (accurate to 0.001 mg). The average fresh weight of third-fourth instar cotton aphids was estimated as 0.043 ± 0.0014 mg. Females and males of *S. levaillanti* were distinguished in terms of colour of their heads (Uygun 1981), while those of *C. sanguinea* were distinguished in terms the shape of their abdominal segment (Gordon, 1985).

Video/Computer Recording and Measurement System

For all experiments, a video/computer recording and measurement system was used to record and analyse the activities of the predators. A complete system consists of a JVC video camera with a lens and an AC adaptor, a video recorder, a personal computer with a monitor and a computer video analysis software (Inchworm) developed at Wye College by Jon Varley in 1989 (Varley et al., 1994). The JVC video camera with a 50 mm SLR camera lens was mounted above the experimental setup to observe the activities of the predator. The camera signal was fed into a video recorder to record all activities on a videotape. During the recording, the video signal was also displayed on the computer monitor to show predator activities in the experimental arena. Afterwards, the recorded videotapes were analysed using Inchworm software.

Experimental Procedure on Timing of Predatory Activities and Relationship between the Prey Consumption and Foraging Cycle

All experimental studies were conducted under laboratory conditions of photoperiod with a continuous light produced by a cold light illumination, a temperature of 25 °C ± 2 °C, and 60 ± 10% relative humidity. In order to determine the duration of predatory activities of adults and larvae of *S. levaillanti* and *C. sanguinea*, a petri-dish containing 240 third-fourth instar cotton aphids on excised cotton leaves was placed under the video camera and a single predator was then released on the cotton leaf. Afterwards, feeding and non-feeding activities of *S. levaillanti* (3 h) and *C. sanguinea* (4 h) were recorded on a videotape. In order to allow the fourth instar larvae and female adults of *C. sanguinea* to complete their second foraging cycle 4 h observation period for *C. sanguinea* had to be used. For each stage of coccinellid species, 5 individuals were used as replicates. Pre-recorded videotapes were analysed to determine the duration of the following activities:

Feeding: The time the predator spent directly handling the prey,

Resting: The time spent in a motionless pause during which there was only an occasional slight movement of the forelegs,

Cleaning: The time spent in one location, during which the predator moved some legs or mouthparts in a cleaning behaviour,

Walking: The time during which the predator was actively moving,

Digestive pause: The time during which predator pauses feeding to digest the preys consumed before search is resumed once it is fully satiated,

Foraging cycle: The time during which several prey items are captured and consumed, followed by a period of digestive pause before search is resumed.

The number and the weight of aphids eaten were also recorded for only fourth instar larvae and female adults of *S. levaillanti* and *C. sanguinea* while the time spent in walking, cleaning, feeding, and resting by those of *S. levaillanti* and *C. sanguinea* was determined by analysing the pre-recorded video types. The weight of the aphids eaten was calculated by multiplying the number of aphids eaten by the average fresh weight of a medium-size cotton aphid (0.043 ± 0.0014 mg, n = 50). In this case, we assume that fourth instar larvae and female adults ingested the whole aphid.

Data Processing and Analysis

Mean time spent in different types of activities (feeding, cleaning, walking, and resting) by adults and larvae of *S. levaillanti* and *C. sanguinea* were analysed using 1-way analysis of variance (ANOVA). The means were separated using the LSD method at 1% level (SAS Institute, 1985).

Results

Sequence and Durations of Predatory Behaviours

Mean times spent (minute) in different types of activities by adults and larvae of *S. levaillanti* and *C. sanguinea* are presented in Tables 1 and 2, respectively. First instar larvae of both species spent the most time in feeding (171.3 and 149.2 min out of 180 and 240 min observation period for *S. levaillanti* and *C. sanguinea,* respectively). The larvae of both species spent significantly more time in feeding compared to adults. Larvae of *S. levaillanti* spent 81.6% to 95.2% of their time in feeding, whereas larvae of *C. sanguinea* spent 34% to 62.1% depending on the larval instars (Figure 1). Thus, larvae of *S. levaillanti* spent a proportionately greater amount of time in feeding compared to *C. sanguinea*. Adults of *S. levaillanti* also spent more time in feeding compared to *C. sanguinea*, with female adults of both species feeding slightly longer than their male counterparts (Table 1 and 2).

Larvae of *S. levaillanti* spent 4.8% to 18.4% of their time in non-feeding activities (cleaning, walking, and resting), whereas larvae of *C. sanguinea* spent 37.9% to 66% of their time in such activities (Figure 1). Adults of

Table 1. Mean time spent (minute ± SE) in different types of activities by adults and larvae of *Scymnus levaillanti* during 3 h observation period (n = 5)·

Stage	Feeding	Cleaning	Walking	Resting	F and P value	LSD value
1st instar	171.3 ± 1.4	2.6 ± 0.3	6.1 ± 1.1	0	F = 9265.7	2.622
	aA	cC	bE	dC	P < 0.0001	
2nd instar	111.9 ± 4.7	2.1 ± 0.4 dC	17.3±1.0 cD	48.6±4.6 bA	F = 216.3	9.916
	aC	dC	cD	bA	P < 0.0001	
3rd instar	140 ± 2.5	2.1 ± 0.3	23.9±2.3	14.1±1.1	F = 1264.7	5.391
	aB	dC	bC	cB	P < 0.0001	
4th instar	147 ± 2.9	3.2 ± 0.3	26.1 ± 2.1	3.8 ± 0.6	F = 1446.9	5.420
	aB	dC	bC	cC	P < 0.0001	
Male	31.2 ± 1.5	51.7 ± 1.7	48.2 ± 2.4	49 ± 2.5	F = 19.9	6.226
adult	bD	aA	aB	aA	P < 0.0001	
Female	34.8 ± 1.4	46.6 ± 1.7	56.1 ± 1.0 aA	42.6 ± 1.7	F = 36.1	4.418
adult	cD	bB	aA	bA	P < 0.0001	
F and P	F = 498.9	F = 567.3	F = 116.9	F = 100	–	–
value	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	–	–
LSD value	7.792	2.955	5.111	6.683	–	–

Different lower case letters indicate significant differences among means within a row for a particular species life stage. Different upper case letters indicate significant differences among means within a column for a particular activity (ANOVA followed by LSD, $\alpha = 0.01$).

Table 2. Mean time spent (minute ± SE) in different types of activities by adults and larvae of Cycloneda sanguinea during 4 h observation period (n = 5).

Stage	Feeding	Cleaning	Walking	Resting	F and P value	LSD value
1st instar	149.2 ± 3.6	19.9 ± 1.7	28.7 ± 1.1	42.3 ± 1.7	F = 739.5	6.631
	aA	dB	cC	bE	P < 0.0001	
2nd instar	122.2 ± 2.6	3.3 ± 0.3	17.2 ± 1.1	95.3 ± 1.7	F = 1195.5	5.044
	aB	dD	cE	bD	P < 0.0001	
3rd instar	70.3 ± 1.5	20.5 ± 1.5	48.8 ± 1.0	100.5 ± 2.8	F= 349.8	5.420
	bD	dB	cA	aD	P < 0.0001	
4th instar	81.5 ± 1.9	13 ± 0.9	35.6 ± 0.8	109.9 ± 2.1	F = 817	4.596
	bC	dC	cB	aC	P < 0.0001	
Male	11.1 ± 1.2	20.6 ± 1.6	24.9 ± 1.8	183.5 ± 2.1	F = 2316.6	5.138
adult	cE	bB	bD	aA	P < 0.0001	
Female	13.3 ± 0.9	25.1 ± 0.6	26.5 ± 1.1	175.2 ± 1.4	F = 5318.9	3.165
adult	eE	bA	bDC	aB	P < 0.0001	
F and P	F = 685.5	F = 40.5	F = 83.7	F = 686.5	–	–
value	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	–	–
LSD value	6.244	3.565	3.451	5.931	–	–

Different lower case letters indicate significant differences among means within a row for a particular species life stage. Different upper case letters indicate significant differences among means within a column for a particular activity (ANOVA followed by LSD, $\alpha = 0.01$).

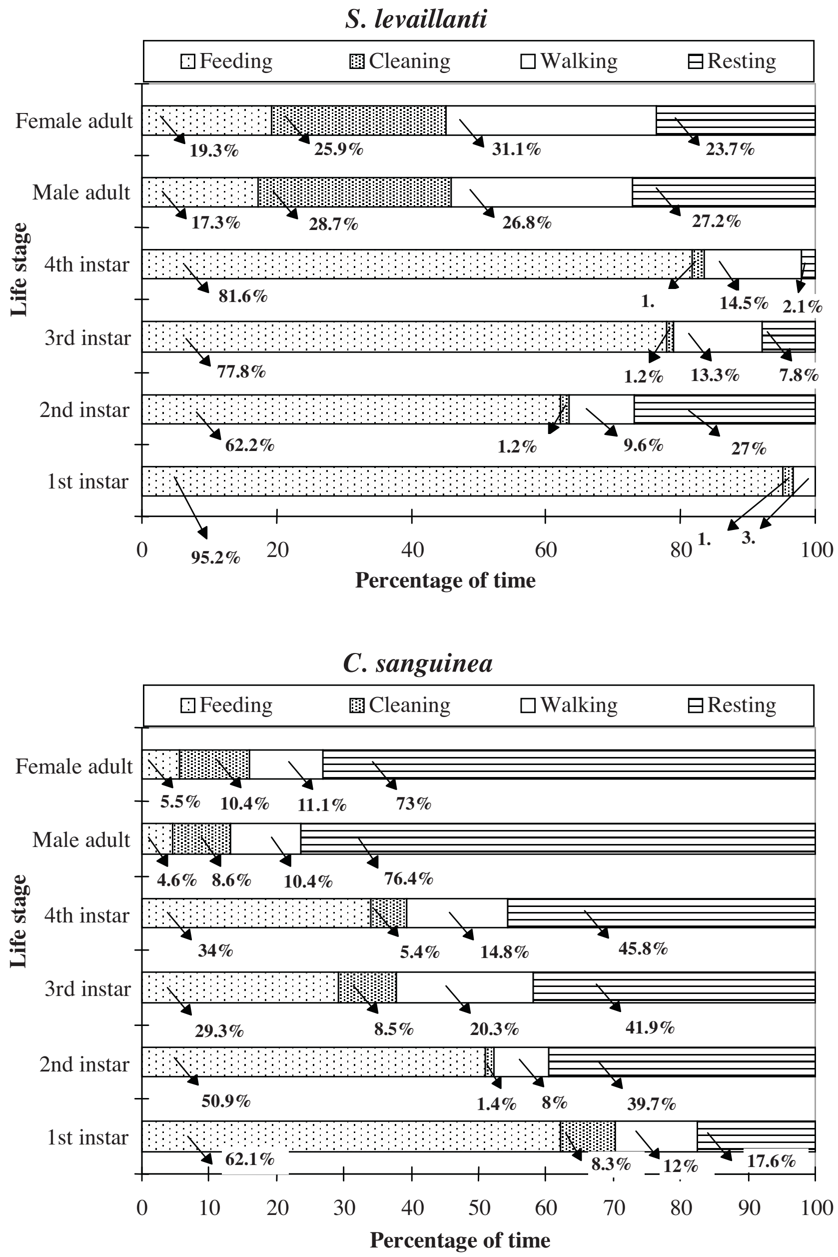

Figure 1. Proportion of time spent by adults and larvae of *S. levaillanti* and *C. sanguinea* in different types of activities during 3 and 4 h observation period, respectively (n = 5).

S. levaillanti and *C. sanguinea* spent more time in non-feeding activities compared to their larvae, whereas adults of *C. sanguinea* spent more time in non-feeding activities compared to *S. levaillanti* (Figure 1). Larvae of *C. sanguinea* were more active compared to *S. levaillanti*, spending more time walking, whereas both male and female adults of *S. levaillanti* were more active compared to *C. sanguinea*. Adults of *C. sanguinea* spent the most time in resting compared to *S. levaillanti* adults, likewise the larvae of *C. sanguinea* spent more time resting compared to *S. levaillanti*. Male adults of *C. sanguinea* spent more time resting and less time in cleaning compared to female adults of *C. sanguinea*. However, male adults of *S. levaillanti* spent more time cleaning compared to female adults of *S. levaillanti* and there was no significant differences in resting time of either sex of *S. levaillanti* (Table 1 and 2).

Relationship Between Prey Consumption and Foraging Cycle

Fourth instars of *S. levaillanti* foraged continuously during the 3 h period, showing no digestive pause (Figure 2). On average, fourth instars of *S. levaillanti* captured and fed 15.4 ± 0.58 aphids (0.6 ± 0.03 mg of aphid, assuming that the predator ingested all of the aphid body), but this was apparently not sufficient consumption to fill the gut to capacity. Thus, fourth instars of *S. levaillanti* were not satiated with 0.6 mg of aphid and did not pause to digest the prey fed. Fourth instars of *S. levaillanti* took a short time to encounter or find each aphid, but spent a long time in feeding it (Figure 2). The attack cycle of fourth instar of *S. levaillanti* (including time spent walking, overcoming, capturing, and feeding) varied from 7 to 18 min.

Fourth instar *C. sanguinea* had an average of 2 foraging cycles with 2 digestive pauses in a 4 h period (Figure 3). Fourth instars of *C. sanguinea* captured and fed an average of 45.2 ± 1.3 aphids (1.8 ± 0.09 mg of aphid) during the first 50 min and, thereafter, entered a digestive pause averaging 30 min. Since the predators were starved for 24 h before the experiment, 1.8 mg most likely represents the maximum gut capacity of fourth instar *C. sanguinea*. These larvae spent a short time walking and cleaning, but a long time feeding. The first foraging cycle lasted for an average of 80 min.

Searching for aphids resumed after the digestive pause, marking the beginning of the second foraging cycle. In the second cycle, they captured and fed an average of 24.4 ± 0.9 aphids (0.96 ± 0.06 mg of aphid) during a period of 50 min and thereafter entered a second digestive pause averaging 80 min. Thus, they consumed less amount of aphid in the second cycle compared to the first, but had a longer digestive pause. In the first foraging cycle, compared to the second foraging cycle, they also spent longer time in feeding, but they spent shorter time in walking and cleaning.

Female adults of *S. levaillanti* had 4 foraging cycles during 3 h period (Figure 4), whereas female adults of *C. sanguinea* had only 2 foraging cycles during 4 h period (Figure 5). Female adults of *S. levaillanti* fed an average of 4.2 ± 0.5 aphids (0.16 ± 0.01 mg of aphid) during the first 30 min, whereupon, they became satiated and entered a digestive pause for 50 min. Presumably, 0.16 mg presents the maximum gut capacity of fourth instars of *S. levaillanti*. The first foraging cycle lasted for 80 min.

In the second foraging cycle, female of *S. levaillanti* fed only 1 ± 0.0 aphid (0.04 ± 0.0 mg of aphid) during a period of 10 min before entering a second digestive pause of 10 min. The second foraging cycle lasted for only

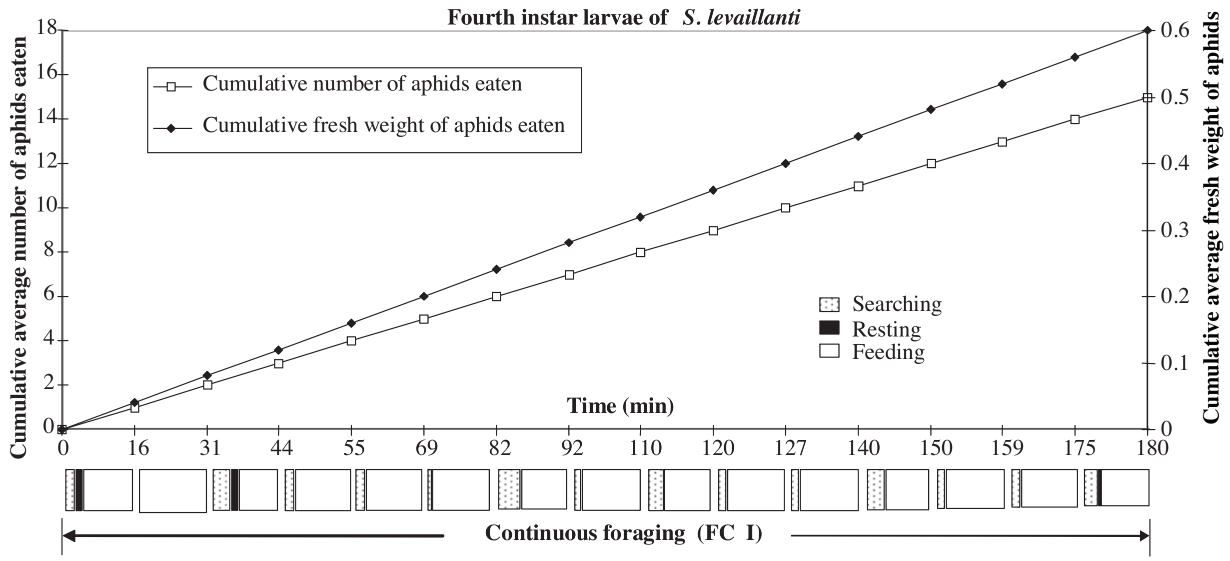

Figure 2. Cumulative average number and weight of the aphids fed over time (minute) spent in various predatory activities by fourth instars of *S. levaillanti* during 3 h observation period (n = 5).

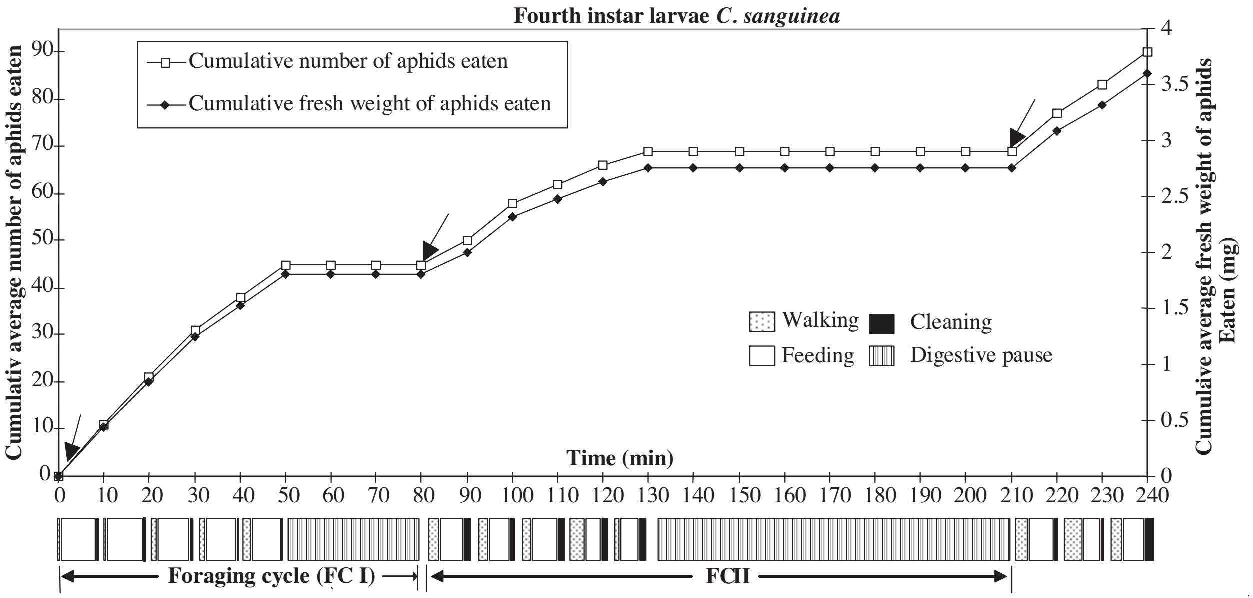

Figure 3. Cumulative average number and weight of the aphids fed over time (minute) spent in various predatory activities by fourth instars of *C. sanguinea* during 4 h observation period (n = 5).

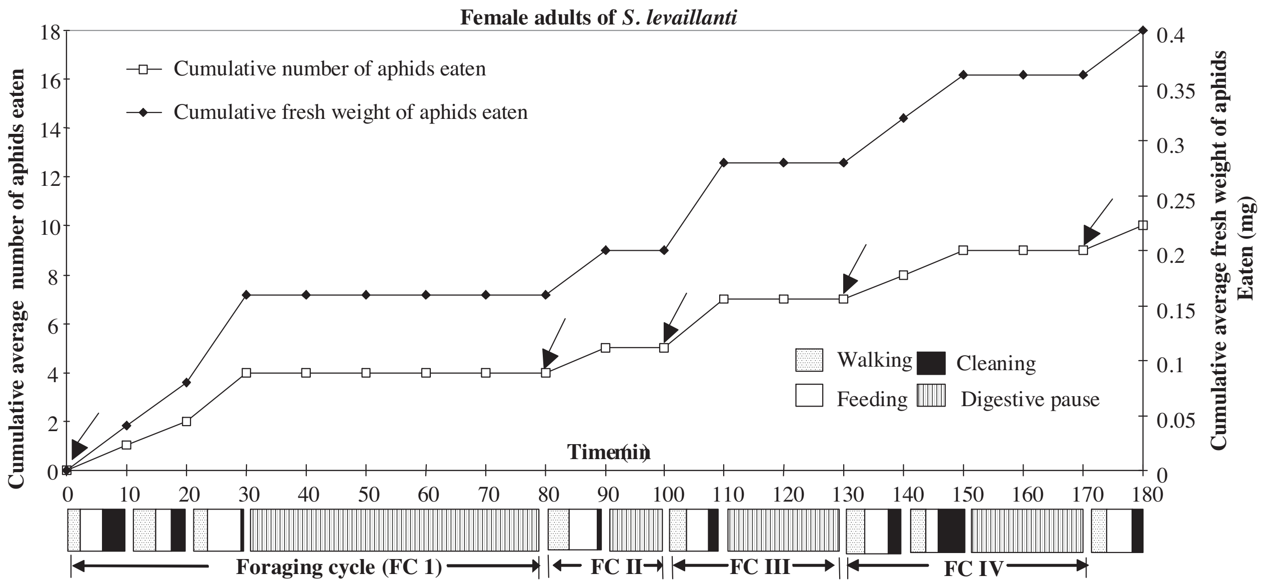

Figure 4. Cumulative average number and weight of the aphids fed over time (minute) spent in various predatory activities by female adults of *S. levaillanti* during 3 h observation period (n = 5).

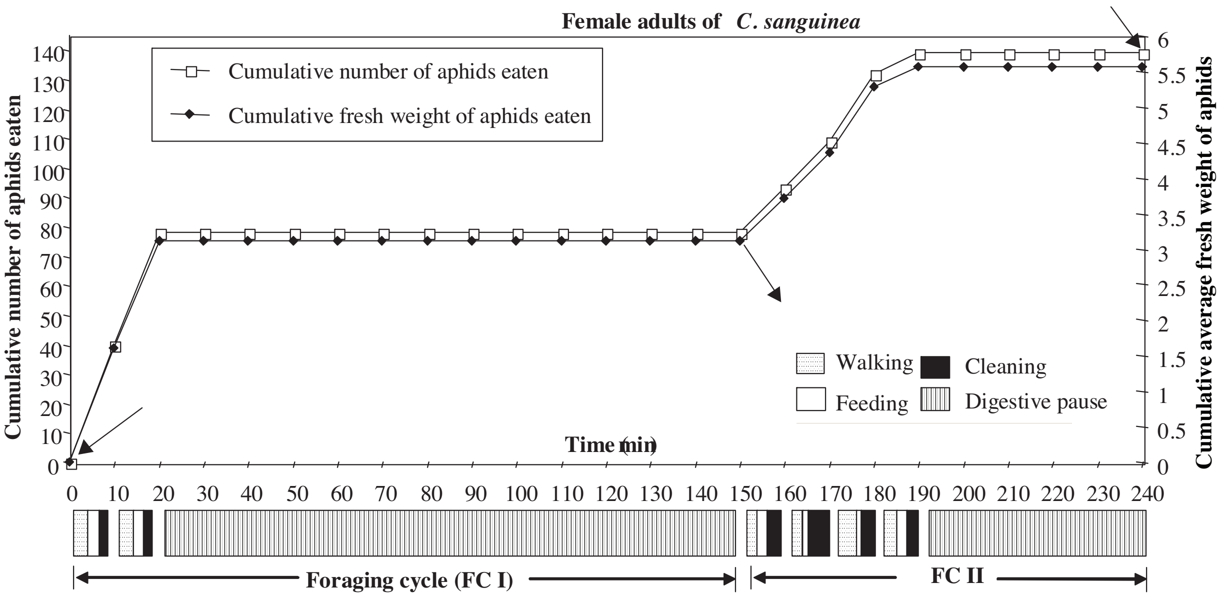

Figure 5. Cumulative number and weight of the aphids fed over time (minute) spent in various predatory activities by female adults of *C. sanguinea* during 4 h observation period (n = 5).

20 min, whereas the third and fourth foraging cycles lasted for 30 and 40 min, respectively. Females fed 2.2 ± 0.03 aphids (0.08 ± 0.005 mg of aphid) during a period of 10 and 20 min, respectively, followed by a digestive pause of 20 min. Thus, female adults of *S. levaillanti* filled and emptied their guts rapidly.

Female adults of *C. sanguinea* had 2 foraging cycles with 2 digestive pauses (Figure 5). In the first foraging cycle, they were fed an average of 78.4 ± 2.6 aphids (3.12 ± 0.3 mg of aphid) during the first 20 min and then entered a digestive pause for 130 min. Thus, the first foraging cycle lasted for 150 min. In this case, 3.12 mg represents the maximum gut capacity of adult female *C. sanguinea*. In the second foraging cycle, they were fed an average of 61 ± 1.3 aphids (2.44 ± 0.25 mg of aphid) during a period of 40 min and then entered into a second digestive pause.

Discussion

Results obtained from video analysis indicated that larvae of *S. levaillanti* spent proportionately more time for feeding compared to *C. sanguinea*. This can be due to the fact that larvae of *S. levaillanti* have a different feeding method with extra-oral digestion (Isikber and Copland, 2000 and 2001). In the case of extra-oral digestion, the larvae periodically regurgitate fluid from the gut into the prey's body and suck back the pre-digested food. Since the predators with extra-oral digestion are able to digest their food during feeding (Cohen, 1984), they spend less time digesting food after consumption, but more time in the feeding process. It seems that the chewing (mastication) method used by larvae of *C. sanguinea* is less time consuming than the extra-oral digestion used by *S. levaillanti*. Similarly, Richards and Goletsos (1991) reported that the sucking and chewing method used by *Coelophora inaequalis* larvae is more efficient and less time consuming than the extra-oral digestion used by *Scymnodes lividigaster*. On the other hand, Isikber and Copland (2001) reported that the larvae of *S. levaillanti*, employing pre-oral digestion, is more efficient in converting food to body mass compared to *C. sanguinea*, which uses chewing and sucking, even though *C. sanguinea* is more voracious than *S. levaillanti*.

The larvae of *C. sanguinea* spent more time in resting compared to *S. levaillanti*, presumably due to the fact that the larvae of *C. sanguinea* have a longer digestion time at more frequent intervals. Adults of both *S. levaillanti* and *C. sanguinea* spent more time in non-feeding activities compared to their larvae, and adults of *C. sanguinea* spent more time in non-feeding activities compared to *S. levaillanti* adults. Adults of *C. sanguinea* spent more time in resting than in any other activity, presumably due to the length of its digestive pause. In accordance with our observations, Johki et al. (1988) reported that the proportion of time spent in resting, feeding, cleaning, and walking differed among 5 Japanese coccinellid species, due mainly to differences in the ratio of resting to walking behaviour. Female adults of *Coccinella septempunctata* L. and *Propylea quatuordecimpunctata* (L.) spent more than 50% of their time in resting. Having a higher time allocation to non-feeding activities has also been observed for other coccinellid species. Nakamuta (1983) reported that female adults of *C. septempunctata* spent 25% of the time in searching and feeding, whereas non-feeding activities, grooming (34% of time) and resting (41% of time), occupied 75% of their total time. Similar results have also been reported for *Adalia decempunctata* L. on black citrus aphid (*Toxoptera aurantii* B.) by Smaili et al. (2006).

Holling and Buckingham (1976) and Mills (1982) suggested that predators have feeding and non-feeding periods that occur in constantly recurring cycles. Hungry predators capture a certain number of preys in succession, followed by a digestive pause associated with satiation. This cycle is repeated several times in a day. Several thresholds seem to be responsible for this behaviour pattern (Holling and Buckingham, 1976). In this study, fourth instars and female adults of both *S. levaillanti* and *C. sanguinea* revealed differences in foraging behaviour in terms of the frequency and duration of their foraging cycles. *S. levaillanti* filled and emptied its gut more rapidly compared to *C sanguinea*. This can be due to *S. levaillanti* requiring fewer aphids to be satiated than *C. sanguinea*, because of a smaller gut capacity. Thus, *S. levaillanti* exhibited more foraging cycles with shorter periods compared to *C. sanguinea* (except fourth instars of *S. levaillanti*). Although *S. levaillanti* spent a longer time in feeding compared to *C. sanguinea*. *S. levaillanti* consumed much lower aphids consumed during observation period compared *C. sanguinea*. Likewise, the higher aphid consumption for *C. sanguinea* compared to *S. levaillanti* has also been previously demonstrated on cotton aphid (Isikber and Copland, 2000 and 2001; Işıkber, 2005).

In conclusion, both coccinellid species show a similar foraging behaviour pattern. Both coccinellid species spend a long period in inactivity (digestion and cleaning) due to satiation, which may have a great impact on the number of aphids consumed daily by these coccinellid species. Clearly, this study may contribute to understand the relationship between prey consumption and foraging cycle of the aphidophagous coccinellids. However, it is necessary to study foraging behaviour of coccinellid predators under field conditions, evaluating the effect of some other factors, in particular prey population density, as well as the size and behaviour of prey.

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