



Original article (Orijinal araştırma)

Cannibalistic behavior of aphidophagous coccinellid, *Hippodamia variegata* (Goeze, 1777) (Coleoptera: Coccinellidae)¹

Afidofag coccinellid, *Hippodamia variegata* (Goeze, 1777) (Coleoptera: Coccinellidae) 'nın kannibalistik davranışları

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Abstract

The variegated lady beetle, *Hippodamia variegata* (Goeze, 1777) is widely distributed in different agroecosystems of Turkey. Cannibalism, intraspecific predation, where individuals of the same species feed upon each other, is a common phenomenon in most aphidophagous coccinellids including *H. variegata*. We investigated the cannibalistic behavior of various growth stages of *H. variegata* in the presence and absence of *Acyrtosiphon pisum* Harris, 1776 under laboratory conditions. The results for cannibalism of eggs and larvae by adults revealed that eggs and younger larvae were more vulnerable to cannibalism. Notably, egg cannibalism by adults was found to be higher even at high prey abundance. Whereas, larval cannibalism was found significantly lower. Cannibalism of eggs by larvae and within the larvae showed that older larvae consumed significantly higher number of eggs and younger larvae in the absence of *A. pisum* indicating that cannibalism was mainly influenced by scarcity of prey. However, all the larval instars, especially 4th and 3rd instars, also consumed a substantial number of eggs even in the presence of prey. Cannibalism within the same stage/age larvae showed a successive increase with the successive larval stage showing minimum cannibalism by 1st instar larvae and maximum by 4th instar larvae. The study found that scarcity of prey leads to cannibalism in *H. variegata* and that egg cannibalism occurs even at high prey densities.

Keywords: *Acyrtosiphon pisum*, cannibalism, eggs, *Hippodamia variegata*, larval instars

Öz

Afidofag coccinellid, *Hippodamia variegata* (Goeze, 1777), Türkiye'nin farklı agroekosistemlerinde yaygın olarak bulunmaktadır. Aynı türün bireylerinin birbirlerine besledikleri kannibalizm, intraspesifik avcılık, *H. variegata* da dahil olmak üzere birçok afidofag coccinellidlerde yaygın olan bir davranıştır. Bu çalışmada laboratuvar koşullarında *Acyrtosiphon pisum* Harris, 1776 varlığında ve yokluğunda *H. variegata*'nın ergin ve ergin öncesi dönemlerine ait kannibalizm davranışları araştırılmıştır. Erginler tarafından yumurta ve larva kannibalizmi üzerine yapılan denemelerde, yumurta ve genç larvanın kannibalizme karşı daha savunmasız olduğunu ortaya koymuştur. İlginç şekilde, erginler tarafından yumurta kannibalizmi, avın bolluğunda dahi belirgin şekilde daha yüksek bulunurken, larva kannibalizmi önemli ölçüde azalmıştır. Larvaların yumurta kannibalizmi ve larva içerisindeki kannibalizm sonuçları, olgun larvaların yaprak biti yokluğunda daha fazla sayıda yumurta ve daha genç yaşta larva tükettiklerini ve avın olmamasının kannibalizme neden olan başlıca etken olduğunu göstermiştir. Bununla birlikte, tüm larva dönemlerinde, özellikle 3. ve 4. larva dönemlerinde, yaprak biti varlığında bile önemli miktarda yumurta tükettikleri saptanmıştır. Aynı yaştaki larvalar arasındaki kannibalizmde, larva dönemleri ile kannibalizm arasında gençlerden yaşlılara doğru olmak üzere doğru orantılı bir korelasyon olduğu belirlenmiştir. Araştırmalarımız, avın azlığının *H. variegata*' da kannibalizm neden olduğunu ancak yumurta kannibalizminin avın yüksek yoğunluklarında bile gerçekleştiğini ortaya koymuştur.

Anahtar sözcükler: *Acyrtosiphon pisum*, kannibalizm, yumurta, *Hippodamia variegata*, larva dönemleri

¹ This study is a part of first author's doctoral research studies. The work was financially supported by Ege University Scientific Research Project No. 2016-ZRF-008.

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Received (Alınış): 22.02.2018 Accepted (Kabul edilmiş): 15.05.2018 Published Online (Çevrimiçi Yayın Tarihi): 06.06.2018

Introduction

The predacious coccinellids (Coleoptera: Coccinellidae) are well-known beneficial insects which are important voracious feeders of many pests of economic importance, like aphids, leaf hoppers, jassids, thrips, whiteflies, scale insects, mealybugs, mites, lepidopteran insects and other soft bodied insects in natural and agricultural habitats (Dixon, 2000; William, 2002; Silva et al., 2009; Khan et al., 2009; Shah & Khan, 2014).

Palaearctic coccinellid species, *Hippodamia (Adonia) variegata* (Goeze, 1777) is a widespread aphidophagous predator in many parts of the world including different agroecosystems of Turkey. It feeds on many insect pests including aphids, whiteflies, jassids, psyllids, mealybugs and lepidopteran insects (Franzman, 2002; Kontodimas & Stathas, 2005). It has been efficiently used in biological control program against a number of insect pests especially aphids. Cannibalism, intraspecific predation, is a well-known behavior of predaceous coccinellids including *H. variegata* and is one of the important mortality factors of coccinellids (Osawa, 1989; Khan et al., 2003; Rondoni et al., 2012; Jafari, 2013).

In aphidophagous coccinellids, cannibalism is an important evolutionary behavior during times of food scarcity that enable them to survive and complete their development. Aphidophagous coccinellids are usually more prone to cannibalism compared to coccidophagous coccinellids as the latter encounter each other less frequently and more likely complete their development before the population collapse of their prey (Agarwala & Dixon, 1992; Dixon, 2000). The eggs and younger larvae appeared to be more helpless against older larvae and adults and are easily devoured (Dimetry, 1974; Hodek, 1996; Nakamura et al., 2006). Cannibalistic behavior of coccinellid adults and older larvae like feeding on eggs, younger or same stage larvae, prepupae/pupae is common in the field. Cannibalism of unhatched eggs in the same egg cluster by the newly hatched first instar larvae is very common and is regarded as sibling cannibalism. This sibling egg cannibalism in ladybirds before dispersion avoid starvation risk and may have adaptive significance in term of increased survival and development by providing essential nutrients and critical energy (Kawai, 1976; Wratten, 1976; Roy et al., 2007).

The adults and larvae of aphidophagous coccinellids have been reported to eat conspecifics in the field (Agarwala & Dixon, 1992; Hindayana et al., 2001; Nakamura et al., 2006; Omkar et al., 2007). The scarcity or presence of extraguild prey greatly influences the intensity of cannibalism (Rosenheim et al., 1995; Lucas et al., 1998; Rondoni et al., 2012). This means that the rate of cannibalism is somehow inversely proportion to the availability of natural food. The abundance of prey also lowers the relative frequency of encounter of adults and older larvae with eggs and smaller larvae leading to minimize the rate of cannibalism (Agarwala & Dixon, 1992; Dixon, 2000; Aleosfoor et al., 2014). However, some research has also revealed cannibalism even in the presence of prey (Osawa, 1989; Agarwala, 1991). Aleosfoor et al. (2014) reported that the rate of cannibalism under starvation was enormously higher in the variegated lady beetle, *H. variegata* compared to satiation conditions and that the rate of cannibalism in *Coccinella septempunctata* (L., 1758) was greater and more frequent than that of *H. variegata*.

A variety of research has been conducted on various aspects of cannibalism in *H. variegata*. However, the present study was designed to conduct detailed investigations on cannibalism in controlled conditions in order to provide a complete set of information on the cannibalistic behavior of *H. variegata* under laboratory conditions.

Material and Methods

Rearing of pea aphid, *Acyrtosiphon pisum*

The pea aphids, *Acyrtosiphon pisum* Harris, 1776 were collected from lucerne and clover and brought to the laboratory. Rearing was maintained on broad bean, *Vicia faba* L., plants grown in sterilized soil in 500 ml pots under laboratory conditions ($23\pm 1^{\circ}\text{C}$ and $65\pm 5\%$ RH).

Rearing of *Hippodamia variegata*

Adults of *Hippodamia variegata* were collected from lucerne, clover, plum, wheat and weeds (grown at the experimental farm of the Faculty of Agriculture, Ege University, Izmir, Turkey) and brought to the laboratory. They were kept in plexiglass cages (20 cm high by 15 cm in diameter) with ventilation holes, two on the side and one in the lid screened with fine mesh. The jars were kept in wooden framed

cage (100 x 70 x 75 cm) in a 16:8 h L:D photoperiod. The aphids were regularly provided to these beetles on their host leaves. The eggs laid by females were collected and transferred to other cages for hatching. Similarly, the larvae emerged from eggs were transferred to plexiglass cages with abundant supply of aphids on leaves. The rearing was maintained at $24\pm 1^\circ\text{C}$, $65\pm 5\%$ RH and 16:8 h L:D photoperiod.

Cannibalism of eggs and larvae by adults

Cannibalism of eggs and larvae by adults was accomplished by keeping 24-h starved male and female (Agarwala & Dixon, 1992) adult beetles individually in Petri dishes (9 cm for eggs and 15 cm for larvae). Each adult (male or female) was provided 100 conspecific eggs with and without 80 aphids, 60 1st instar larvae newly emerged from eggs with and without 350 aphids, or 35 2nd instar larvae with and without 350 aphids for 24 h. The experiments included 10 replicate adult males and females for each treatment. Petri dishes were examined after 24 h for evidence of cannibalism.

Cannibalism of eggs by larvae

In this experiment all the four larval instars were kept individually in Petri dishes (9 cm) and starved for 12 h to standardize their appetite (Yasuda et al., 2001; Khan et al., 2003). Known numbers of the conspecific eggs were transferred with the help of soft camel hair brush to the Petri dishes. The different numbers of conspecific eggs presented to each larval instar were: 1st instar 20 eggs, 2nd instar 30, 3rd instar 40 and 4th instar 100. The number of eggs consumed by larvae was recorded after 24 h. In another experiment the same number of conspecific eggs were provided to all the four larval instars along with different densities of aphids (20, 30, 40 and 80 for 1st, 2nd, 3rd and 4th instars, respectively) in order to record cannibalism in the presence of natural food. All treatments in the experiments consisted of 10 replicates.

Cannibalism within the larval stages

To determine cannibalism within larvae, two experiments were conducted. In first experiment cannibalism of younger larvae by older was investigated in the presence and absence of aphids. The 4th, 3rd and 2nd larval instars were kept singly in 15-cm Petri dishes and starved for 12 h to standardize their appetite. Well-fed 1st and 2nd larval instars (60 and 35, respectively) were provided with 4th instar larvae in separate Petri dishes in the presence (350 aphids for each of 1st and 2nd instars) and absence of aphids. Similarly, 1st and 2nd instar larvae (35 and 20, respectively) were provided with 3rd instar larvae in the presence (250 aphids for each of 1st and 2nd instars) and absence of aphids, and 20 1st instar larvae were given to 2nd instar larvae ($n = 10$) with and without 100 aphids. Examination for evidence of cannibalism was made after 24 h. In the second experiment, same age larvae of each stage (1st, 2nd, 3rd and 4th) were starved for 12 h as above and then kept together for 24 h in 12-cm Petri dishes in the presence and absence of prey. The aphid densities provided were 70, 100, 250 and 500 aphids for each of the Petri dishes with 10 1st, 2nd, 3rd and 4th larval instars, respectively.

The cannibalistic behavior of *H. variegata* was studied at $24\pm 1^\circ\text{C}$ and 16:8 h L:D photoperiod. Similar aged adult beetles (male and female), different larval instars and eggs used in the experiments were taken from stock culture maintained on *A. pisum*.

Statistical analysis

Data on the cannibalistic behavior of *H. variegata* were subjected to one-way analysis of variance using statistical software SPSS, 2008. Multiple comparison among the means was made using Tukey's HSD test ($P < 0.05$). Independent sample t-test was used where two variables were involved.

Results and Discussion

Cannibalism of eggs by adults

The data on cannibalism of eggs by adult male and female of *H. variegata* revealed that females consumed significantly higher mean number of eggs (95.3 ± 1.53) than males (52.7 ± 1.39) in the absence of aphids (Figure 1) The availability of high density of *A. pisum* resulted in a significant reduction in the conspecific egg consumption, however, it was still substantially higher especially for females, which consumed significantly more eggs (32.8 ± 1.86) than males (19.4 ± 1.59) ($F = 427.23$, $df = 3$, $P < 0.001$).

Cannibalism of 1st and 2nd instar larvae by adults

The data on cannibalism of 1st and 2nd instar larvae by adult males and females of *H. variegata* revealed that both the sexes were voracious towards 1st instar larvae. However, adult females showed a more vigorous response towards 1st and 2nd instar larvae in absence of aphids, consuming on average 52.5 ± 1.5 and 31.5 ± 0.9 larvae, respectively, which was significantly greater than that of adult males (46.2 ± 1.59 and 26.3 ± 0.76 , respectively) ($F = 455$, $df = 7$, $P < 0.001$). The presence of aphids caused a drastic reduction in consumption of larvae and negligible amounts of 1st and 2nd instar larvae were consumed by both adult females and males (Figure 2).

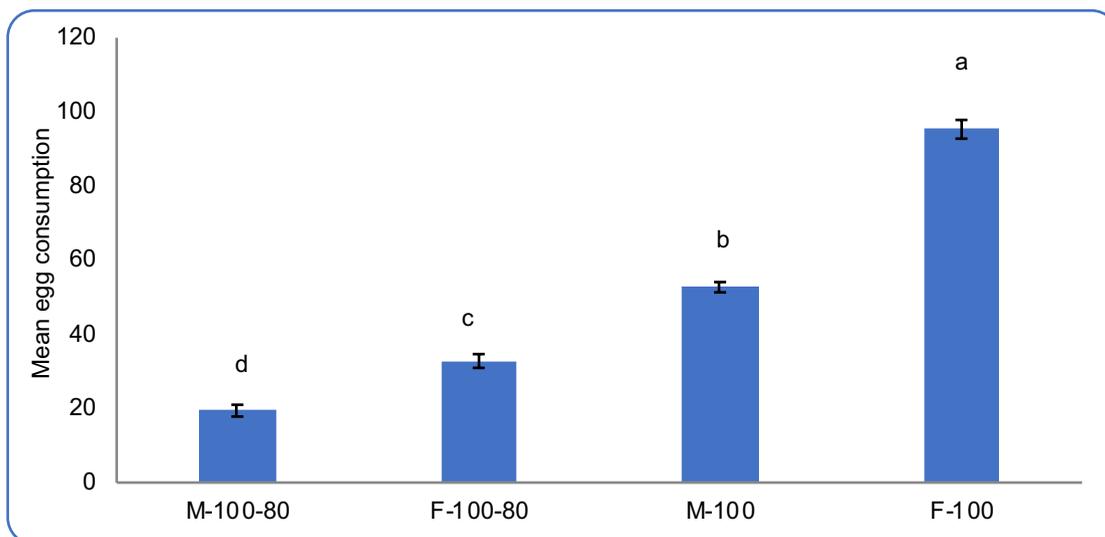


Figure 1. Cannibalism of conspecific eggs by adult male and female of *Hippodamia variegata*. Each bar represents mean egg consumption (\pm SEM). M-100 = 100 eggs provided to adult males, F-100 = 100 eggs provided to adult females, M-100-80 = 100 eggs along with 80 *Acyrtosiphon pisum* provided to males, and F-100-80 = 100 eggs along with 80 *A. pisum* provided to females. Different letters above the bars indicate significant differences ($P < 0.05$).

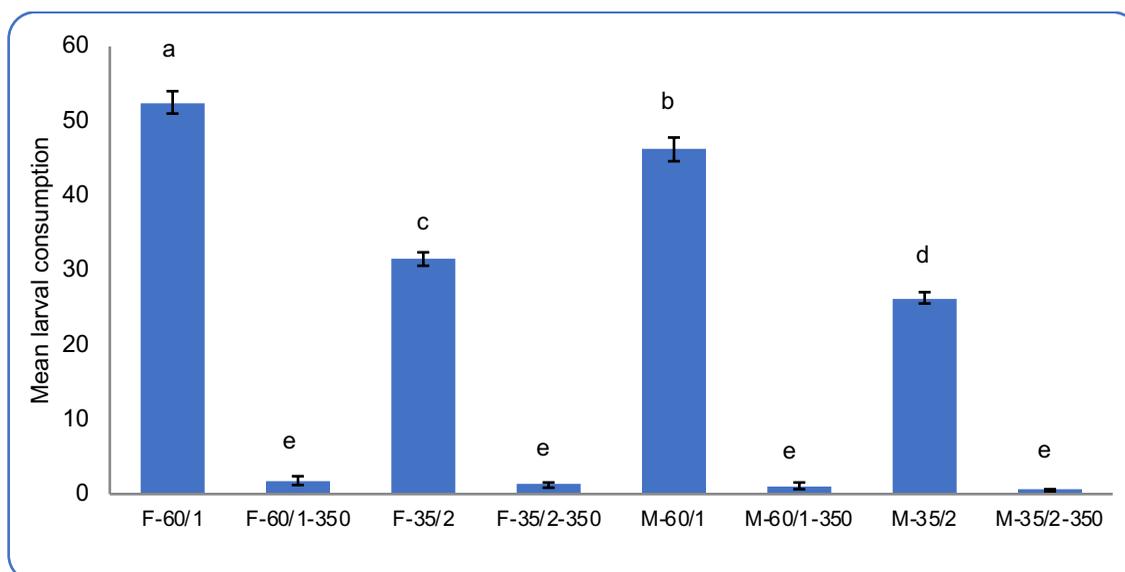


Figure 2. Cannibalism of 1st instar and 2nd instar larvae by male and female of *Hippodamia variegata*. F-60/1 = 60 1st instar larvae provided to adult females, F-60/1-350 = 60 1st instar larvae provided to adult females along with 350 *Acyrtosiphon pisum*, F-35/2 = 35 2nd instars provided to females, F-35/2-350 = 35 2nd instar larvae provided to females along with 350 *A. pisum*, M-60/1 = 60 1st instars provided to adult males, M-60/1-350 = 60 1st instar larvae provided to male with 350 *A. pisum*, M-35/2 = 35 2nd instars provided to males, and M-35/2-350 = 35 2nd instar larvae provided to male along with 350 *A. pisum*. Different letters above the bars indicate significant differences ($P < 0.05$).

Cannibalism of eggs by larvae

The rate of cannibalism by the four larval instars of *H. variegata* on the conspecific eggs varied greatly with significant differences among the different growth stages (Figure 3). In the absence of prey, 4th instar larvae proved to be the most voracious consuming significantly higher number of eggs (86.1 ± 1.89), followed by 3rd instar larvae (29.4 ± 1.22), during the 24-h exposure period ($F = 451$, $df = 7$, $P < 0.001$). The presence of aphids significantly reduced egg consumption by all the larval instars, however, the 4th instar larvae showed some degree of preference for the eggs even in presence of aphids consuming 25.8 ± 2.4 eggs. The 3rd instar larvae consumed 9.37 ± 0.84 eggs in the presence of aphids, this was not significantly different from the number of eggs consumed by 2nd instar larvae in the absence of aphids (11.6 ± 0.86). The lowest number of eggs was consumed by the 1st instar larvae (5.37 ± 0.46), but this was insignificantly different from its consumption of eggs in presence of aphids (2.37 ± 0.56) (Figure 3).

Cannibalism within larvae

The data on cannibalism of younger larvae by older larvae of *H. variegata* revealed that all the starved older larval stages voraciously fed on younger larvae (Figure 4). The 4th instar larvae consumed a significantly higher number of 1st and 2nd instar larvae (51.7 ± 1.55 and 29.7 ± 1.10 , respectively) in absence of prey followed by 3rd instar larvae with average consumption of 26.8 ± 1 and 16.7 ± 0.66 , respectively ($P < 0.05$). The 2nd instar larvae consumed significantly less 1st instar larvae (5.1 ± 0.31) in absence of *A. pisum* ($F = 548$, $df = 9$, $P < 0.001$). The presence of a high density of aphids caused a marked reduction in larval consumption by the 2nd, 3rd and 4th instars with only a negligible number of larvae consumed (Figure 4).

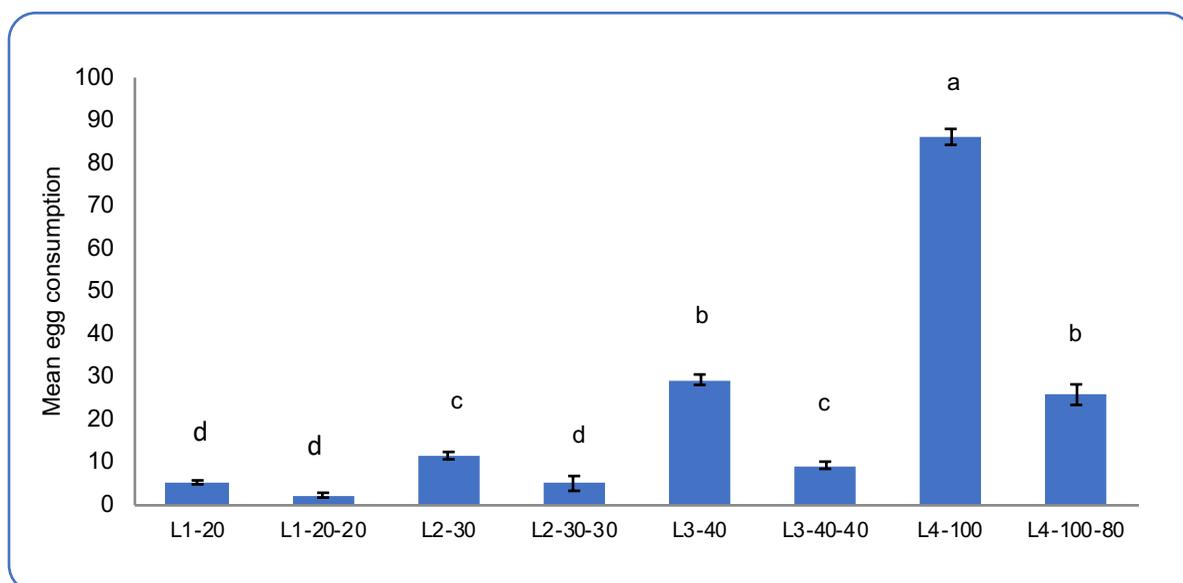


Figure 3. Cannibalism of eggs by different larval instars of *Hippodamia variegata* in the presence and absence of aphids. L1-20 = 20 eggs provided to 1st instars, L1-20-20 = 20 eggs along with 20 *Acyrtosiphon pisum* provided to 1st instars, L2-30 = 30 eggs provided to 2nd instars, L2-30-30 = 30 eggs along with 30 *A. pisum* provided to 2nd instars, L3-40 = 50 eggs provided to 3rd instars, L3-40-40 = 50 eggs along with 60 *A. pisum* provided to 3rd instars, L4-100 = 100 eggs provided to 4th instars, L4-100-80 = 100 eggs along with 80 *A. pisum* provided to 4th instars. Different letters above the bars indicate significant differences ($P < 0.05$).

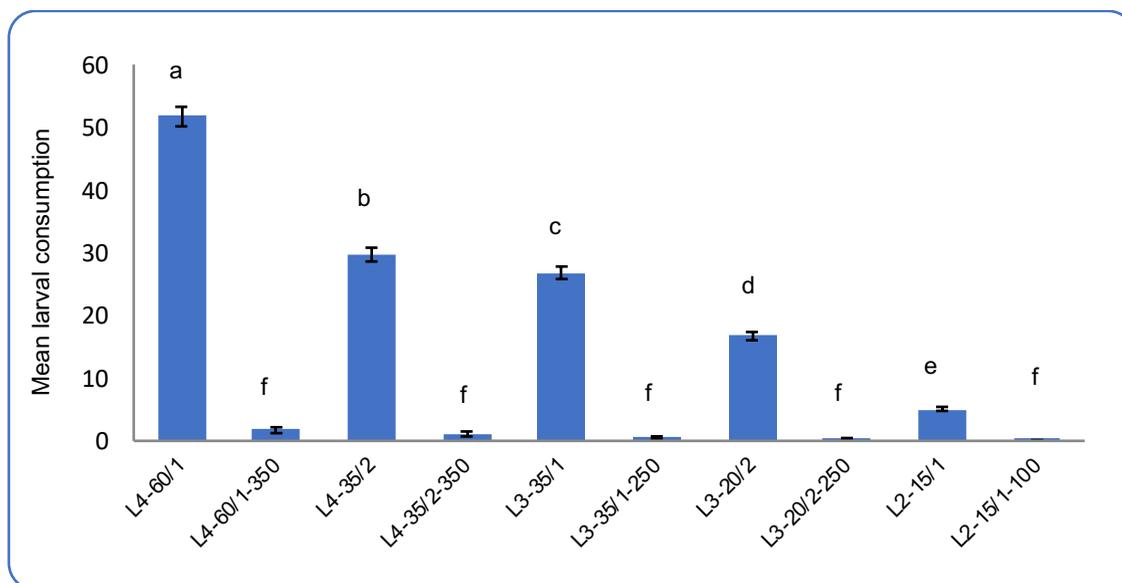


Figure 4. Cannibalism of younger larvae by older ones. L4-60/1 = 60 1st instars provided to 4th instars, L4-60/1-350 = 60 1st instars provided to 4th instars with 350 *Acyrtosiphon pisum*, L4-35/2 = 35 2nd instars provided to 4th instars, L4-35/2-350 = 35 2nd instars provided to 4th instars along with 350 *A. pisum*, L3-35/1 = 35 1st instars given to 3rd instars, L3-35/1-250 = 35 1st instars provided to 3rd instars with 250 *A. pisum*, L3-20/2 = 20 2nd instars provided to 3rd instars, L3-20/2-250 = 20 2nd instars given to 3rd instars with 250 *A. pisum*, L2-15/1 = 15 1st instars provided to 2nd instars, and L2-15/1-100 = 15 1st instars provided to 2nd instars along with 100 *A. pisum*. Different letters above the bars indicate significant differences ($P < 0.05$).

Cannibalistic behavior of the same age larvae of *H. variegata* in the absence of *A. pisum* increased successively with larval stage. The highest ($P < 0.05$) cannibalism rate of 3.7 ± 0.30 was recorded for 4th instar larvae. The rate of cannibalism within 3rd (2.8 ± 0.29) and 2nd instar larvae (2.6 ± 0.33) was not significantly different. The same was the lowest ($P < 0.05$) for the 1st instar larvae (1.7 ± 0.42). In the presence of aphids, cannibalism was negligible and not statistically different between the same age larvae of the 4 instars (Figure 5).

These results revealed that cannibalism in *H. variegata* took place mainly when aphid prey was scarce and the predators were starving. Eggs and younger larvae appeared to be the most vulnerable stages which were consumed in large numbers by both the adults and older larvae. Many researchers report that egg and younger larval cannibalism is a widespread phenomenon in predacious ladybirds (Takahashi, 1987; Osawa, 1989, 1992; Agarwala & Dixon, 1992; Kajita et al., 2010). The sibling cannibalism where newly hatched larvae in the same egg cluster cannibalize the sibling unhatched eggs is also well known in the ladybirds (Hodek, 1996; Agarwala, 1991). A cannibalizing predator has an advantage by increasing its chances of survival in times of food scarcity, and also by killing or eradication of a potential competitor sharing similar resources.

Our results confirmed that all the growth stages fed on the conspecifics in the absence of aphids indicating that the presence or absence of alternative food source influences the frequency of cannibalism (Osawa, 1989; Burgio et al., 2002). Whereas, the provision of high density of natural prey led to a marked reduction in the rate of cannibalism by all the growth stages of *H. variegata*. This is consistent with the findings of Agarwala (1991) and Aleosfoor et al. (2014), who reported that collapse of the aphid population in an ecosystem exerts great pressure on larvae and adults of coccinellids to survive, consequently unhatched eggs or minor larvae become the readily available food source.

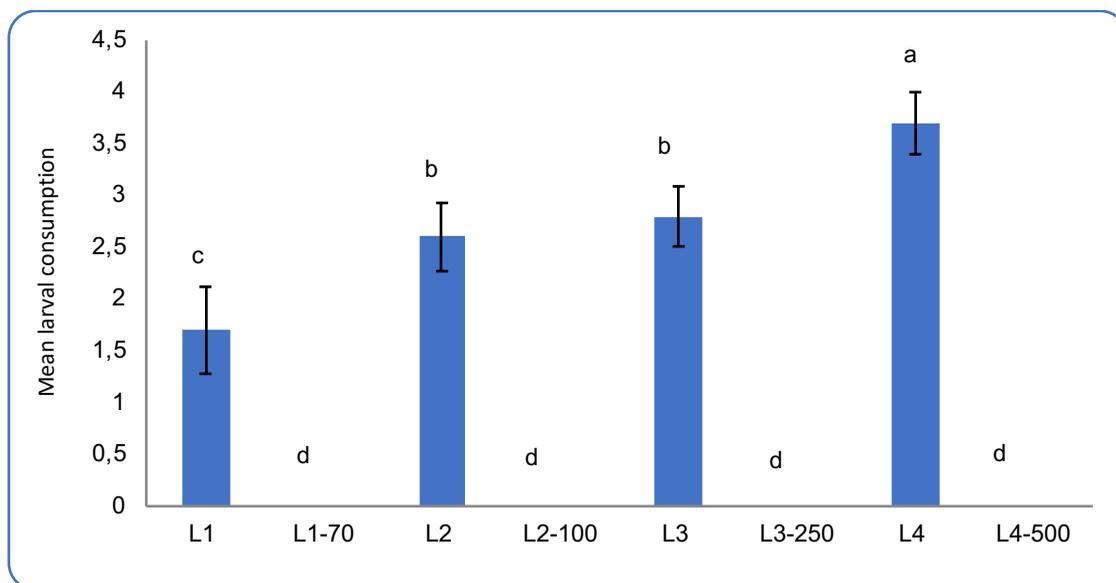


Figure 5. Cannibalism within the same age larvae. L1 = 10 1st instars alone, L1-70 = 10 1st instars along with 70 aphids, L2 = 10 2nd instars alone, L2-100 = 10 2nd instars along with 100 aphids, L3 = 10 3rd instars alone, L3-250 = 10 3rd instars along with 300 aphids, L4 = 10 4th instars alone, and L4-500 = 10 4th instars along with 500 aphids. Different letters above the bars indicate significant differences ($P < 0.05$).

Adult females appeared to be more voracious towards eggs and younger larvae in the absence of prey followed by 4th instar larvae and adult males. The egg consumption of males was, however, far lower than that of adult females and 4th instar larvae (Figure 1). The greater voracity of these growth stages for conspecific eggs and larvae can be attributed to their larger size (Agarwala & Dixon, 1992; Cottrell, 2005; Sato et al., 2011; Lucas, 2012; Jafari, 2013) and higher nutritional requirements, especially in case of reproductive females and 4th instar larvae completing their development (Fox, 1975; Polis, 1981; Takahashi, 1987; Hodek & Honek, 1996).

It is noteworthy that all the growth stages of *H. variegata* showed some degree of preference for the conspecific eggs even when there was an abundance of prey. The number of eggs eaten by 1st instar larvae in the absence of aphids was not significantly different than when aphids were present. Adult females and males, and 4th instar larvae, in particular, consumed substantial amount of the conspecific eggs even in the presence of aphids, with the most voracious response exhibited by adult females. This could be attributed to eggs being immobile and unable to escape (Takahashi, 1987; Agarwala, 1991; Hodek & Honek, 1996). Agarwala (1991) reported higher rates of egg cannibalism in ladybirds at lower prey densities. Also, non-sibling cannibalism of eggs in ladybirds mostly happens without the influence of prey availability (Fox, 1975; Polis, 1981; Mills, 1982; Osawa, 1989).

The phenomenon of egg cannibalism in ladybirds, including *H. variegata*, has also been regarded as a mean of nutritional and energetic gains in term of larger body size, faster development, earlier maturity, competitive advantage in mating and higher rate of reproduction (Osawa, 1992; Felix & Soares, 2004; Michaud & Grant, 2004; Omkar et al., 2004; Pell et al., 2008; Rondoni et al., 2014). Poor diet quality also exerts pressure on predators to feed on their conspecifics. However, there appears to be no published information on the nutritional quality of *A. pisum* for *H. variegata* or other coccinellids.

The higher egg consumption by females in the presence of prey also indicates that the females are more sensitive than males to resource limitation, and hence get maximum benefit from egg cannibalism. Another reason could be the higher amount of energy required by female for reproduction (Michaud & Grant, 2004). There is also some evidence that the coccinellids do not tend to lay their eggs close to the

aphid colony (Banks, 1954; Dixon, 1959; Osawa, 1989) as near the aphid colony the risk of being cannibalized is higher (Osawa, 1989). However, Dixon (1959) reported that ladybirds will oviposit in the vicinity of an aphid colony to enable their progeny to easily access the food. Cannibalism of eggs by the adults and larvae has also been widely recorded in the field in several species of ladybirds (Mills, 1982; Takahashi, 1989).

It is also worth noting that coccinellid eggs are protected from predation by the presence of defensive alkaloids and other chemicals. Hemptinne et al. (2000) reported many compounds found on the egg surface of *Adalia bipunctata* (L. 1758) and *C. septempunctata*, which serve to reduce predation by other coccinellid predators. However, in most coccinellids egg cannibalism is widespread as there are no disadvantages linked with the consumption of conspecific eggs with a positive impact on development and survival (Felix & Soares, 2004; Ware & Majerus, 2008; Kajita et al., 2010). Similarly, Osawa (1989), Agarwala (1991), Agarwala & Dixon (1992), Agarwala et al. (1998), Michaud (2002), Omkar et al. (2006), Ware & Majerus (2008) and Kajita et al. (2010) reported that the coccinellid predators tend to prey on conspecific eggs instead of heterospecific eggs. This may probably be due to the occurrence of alkanes and alkaloids on the surface of conspecific eggs. These surface chemicals seemingly act as feeding attractants for individuals of same species and hence increase cannibalism to some extent (Omkar et al., 2004).

Base on the data collected, it is concluded that cannibalism in *H. variegata* is inversely proportional to the availability of prey. Adult females and males, and 4th instar larvae are voracious feeders of eggs and younger larvae, and that egg cannibalism occurs irrespective of the aphid presence.

Acknowledgments

The authors are highly thankful to Prof. Dr. Ferit Turanlı (Ege University, Faculty of Agriculture, Department of Plant Protection, İzmir, Turkey) and Prof. Dr. İsmail Karaca (Süleyman Demirel University, Faculty of Agriculture, Department of Plant Protection, Isparta, Turkey) for their valuable guidance and suggestions. This work was financially supported by Ege University Scientific Research Project No. 2016-ZRF-008.

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