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Phenology, fecundity and life table parameters of the predator *Hippodamia variegata* reared on *Dysaphis crataegi*

D.C. KONTODIMAS[1] and G.J. STATHAS[2,*]
[1]*Benaki Phytopathological Institute, Laboratory of Biological Control, 8 S. Delta Str., GR 145 61 Kifissia, (Athens) Greece;* [2]*Technological Educational Institute of Kalamata, School of Crop Production, GR 24 100 Antikalamos (Messinia) Greece*
**Author for correspondence; e-mail: georgestathas@teikal.gr*

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Abstract. Phenological and some biological characteristics of *Hippodamia* (*Adonia*) *variegata* (Goeze) (Coleoptera: Coccinellidae), such as voltinism, hibernation, number of progeny produced by each generation, mating activity and sex ratio were studied, in order to evaluate the significance of this predator. The study of phenology was conducted in outdoor cages in Kifissia (Athens), during 1999–2001 and as prey was given *Dysaphis crataegi* (Kaltenbach). *Hippodamia variegata* completed seven generations between April and November. The hibernating population of *H. variegata* consisted of adults of 6th and 7th generations. The fecundity of the predator was studied under constant conditions [25 °C, 65% R.H. and 16:8(L:D)h photoperiod] in the laboratory and some population parameters were calculated: The total fecundity ranged between 789 and 1256 eggs, while the mean total fecundity was 959.6 eggs. The greatest proportion of eggs (45%) was oviposited in clutches of 11–20 eggs. The net reproductive value (R_0) was found to be 425.9 females/female, the intrinsic rate of increase (r_m) 0.178 females/female/day and the mean generation time (T) 34.0 days.

Key words: Coccinellidae, Coleoptera, *Dysaphis crataegi*, fecundity, *Hippodamia* (*Adonia*) *variegata* (Goeze) (Coleoptera: Coccinellidae), Greece, life table, phenology

Introduction

The Palaearctic coccinellid species *Hippodamia* (*Adonia*) *variegata* (Goeze) is a widespread aphidophagous predator that has been established successfully in America and Canada (Gordon, 1987; Krafsur et al., 1996; Wheeler and Stoops, 1996). It has been reported as the most important natural enemy of aphids infesting various crops, in many countries. It has been cited as the most important predator against aphids on pepper in Bulgaria (Natskova, 1973), on maize in Ukraine (Gumovskaya, 1985), on shrubs in Italy (Nicoli et al., 1995), on grain in India (Hammed et al., 1975) and on cotton on Turkmenistan (Belikova and Kosaev, 1985). *Hippodamia variegata* was also the most abundant predator and represented 64.5% of the total number of coccinellid individuals found on cotton infested by *Aphis gossypii* Glover (Kavallieratos et al., 2002). Apart from predating aphids, it has been recorded feeding on other sucking insects (Alan, 1979), Cicadellids (Singh et al., 1991), larvae of Curculionidae and pollen (Sadeghi and Esmailli, 1992).

Limited data concerning the biology or ecology of *H. variegata* are available. Most of them deal with the prey consumption of the predator (Fan and Zhao, 1988; Obrycki and Orr, 1990; Kalushkov et al., 1991; Sadeghi and Esmailli, 1992; Singh and Singh, 1994) or with the effect of temperature on the larval development of *H. variegata* (Michels and Bateman, 1986; Michels and Flanders, 1992; El Habi et al., 2000). Because of lack of information about the biology of *H. variegata* in Greece the following study was conducted to obtain data about voltinism, longevity and fecundity, factors that may be used to evaluate the effectiveness of Coccinellidae indirectly (Hodek, 1973). Rearing of *H. variegata* in outdoor cages took place in order to study its phenology (voltinism, longevity, hibernation, the number of progeny produced from each generation, mating activity, and sex ratio). Fecundity in laboratory conditions was also examined to obtain the average total fecundity as well as the life table parameters (age specific survival and fecundity, reproductive value, excepted remaining life time, net reproductive value, intrinsic rate of increase, mean generation time, finite rate of increase, doubling time and stable age distribution). The above parameters are essential to estimate the rate of increase of a natural or released population (El Hag and Zaitoon, 1996) as well as the appropriate time for release of a laboratory-reared population.

Materials and methods

Study of phenology in semi-natural conditions

Adults of *H. variegata,* emergent from 50 larvae collected from orange trees infested by aphids in Athens, were used to initiate the first generation. Larvae were reared together in a cylindrical Plexiglas cage (30 cm in diameter, 50 cm in length) placed outdoors in foliar shadow near the laboratory of Benaki Phytopathological Institute, Kifissia, Athens, during 1999–2001. *Dysaphis crataegi* (Kaltenbach) infesting squashes of *Cucurbita maxima* Duchense was provided as prey twice per week. Successive generations were separated from one another by moving the first 50 neonates from each generation into a new cage. The rest of the larvae were counted and then removed from the cages. Dead larvae were substituted by others of the same generation and the same instar, so as to always begin with 50 adults in the next generation. This was repeated until all initiatory adults of each generation died. The number of living adults, eggs and larvae in each cage were recorded twice per week. Simultaneously with the above observations all matings, which at that time occurred, were also recorded. In addition, to calculate the percentage of females of *H. variegata* that were actively reproductive in each generation, 20 females from each generation were reared in male–female pairs in outdoor cylindrical cages (16 cm in length × 5 cm in diameter) until the start of oviposition. Data on daily temperatures were obtained by a weekly thermograph recorder (Thiesclima; model 0177) placed in a meteorological cage located in Benaki Phytopathological Institute. The temperature in the meteorological cage was ascertained to be the same as the temperature inside the cylindrical cages. In the same place and under the same outdoor conditions the phenology of other native coccinellids was also studied in the past (Katsoyannos et al., 1997a, b, d).

Study of fecundity in the laboratory

In order to study the fecundity of *Hippodamia variegata*, 25 newly emerged pairs of adults of the predator were reared under constant conditions of 25 ± 1 °C, 65 ± 2% relative humidity and 16:8(L:D)h photoperiod. Life table parameters of other coccinellid species have been studied in similar conditions in east Mediterranean (Uygun and Elekcioglu, 1998; Uygun and Atlihan, 2000). Each pair was reared separately in a plastic cylindrical cage (10 cm diameter and 5 cm height) and pieces of pumpkin heavily infested with *D. crataegi* were provided as a food source every day. Survivals of the immature stages and sex ratio of the progeny were estimated under the same conditions. Female longevity and fecundity were measured and the following table parameters were calculated:

– the age specific survival (l_x) of the 25 females,
– the age specific fecundity (m_x) (= born females/female), obtained by multiplying the mean number of eggs by 0.58, the ratio of females to total eggs (Liu et al., 1997)
– the net reproductive value:

$$R_0 = \sum (l_x \cdot m_x) \quad \text{(Birch, 1948; Izhevsky and Orlinsky, 1988)}$$

– the intrinsic rate of increase (r_m), which is calculated by iteratively solving the Euler equation,

$$\sum (e^{-r_m \cdot x} \cdot l_x \cdot m_x) = 1 \quad \text{(Birch, 1948)}$$

– the mean generation time:

$$T = \frac{\ln R_0}{r_m} \quad \text{(Birch, 1948; Chazeau et al., 1991; Kairo and Murphy, 1995)}$$

– the finite rate of increase:

$\lambda = e^{r_m}$ (Birch, 1948)

– the doubling time:

$$DT = \frac{\ln 2}{r_m} \quad \text{(Kairo and Murphy, 1995)}$$

– the reproductive value of the females:

$$V_x = \frac{\sum_{y=x} (e^{r_m \cdot y} \cdot l_y \cdot m_y)}{l_x \cdot e^{-r_m \cdot x}} \quad \text{(Imura, 1987)}$$

– the expected remaining life time of the females:

$$E_x = \frac{\sum_{y=x} \frac{l_y + l_{y+1}}{2}}{l_x} \quad \text{(Southwood, 1966) and}$$

– the stable age distribution:

$$C_x = \frac{l_x \cdot e^{-r_m \cdot x}}{\sum_{x=0} (l_x \cdot e^{-r_m \cdot x})} \quad \text{(Birch, 1948)}$$

Furthermore, the proportion of the eggs laid in clutches of 1–10, 11–20, 21–30 and >30 eggs, was measured.

Results

Phenology in outdoor cages

Hippodamia variegata completed seven generations from May 1999 to April 2000 and from May 2000 to April 2001 (Figure 1). Table 1 shows the mean longevity of each generation. Adults of the 1st, 2nd and 3rd generations lived until the autumn (September–October) in both years of the study (Figure 1). Adults of the 4th and 5th generation died during winter (December–January), whereas adults of the 6th and 7th generation survived winter conditions and lived until the following May. The sex ratio of each generation ranged from 1:1 to 1:1.3 (males:females) (Table 1).

The number of matings (Figure 1), does not correspond to the actual number of matings but to that observed during cage inspection. Matings were recorded as an indication of reproductive activity and were observed during cage inspections throughout adulthood in all generations. By rearing 20 pairs of each generation in a separate cage, it was confirmed that all females laid eggs. In the 1st year (1999–2000) the average fecundity of *H. variegata* (eggs and hatched larvae) ranged from 82.0 to 294.4 progeny per female, while during the 2nd year (2000–2001) it ranged from 76.3 to 246.0 (Table 1). Eighty-three percent of the progeny of 6th generation and 36% of the progeny of 7th generation appeared before the winter of 1999–2000, whereas the rest were recorded after that. Similarly, in the second year of the study 80% of the

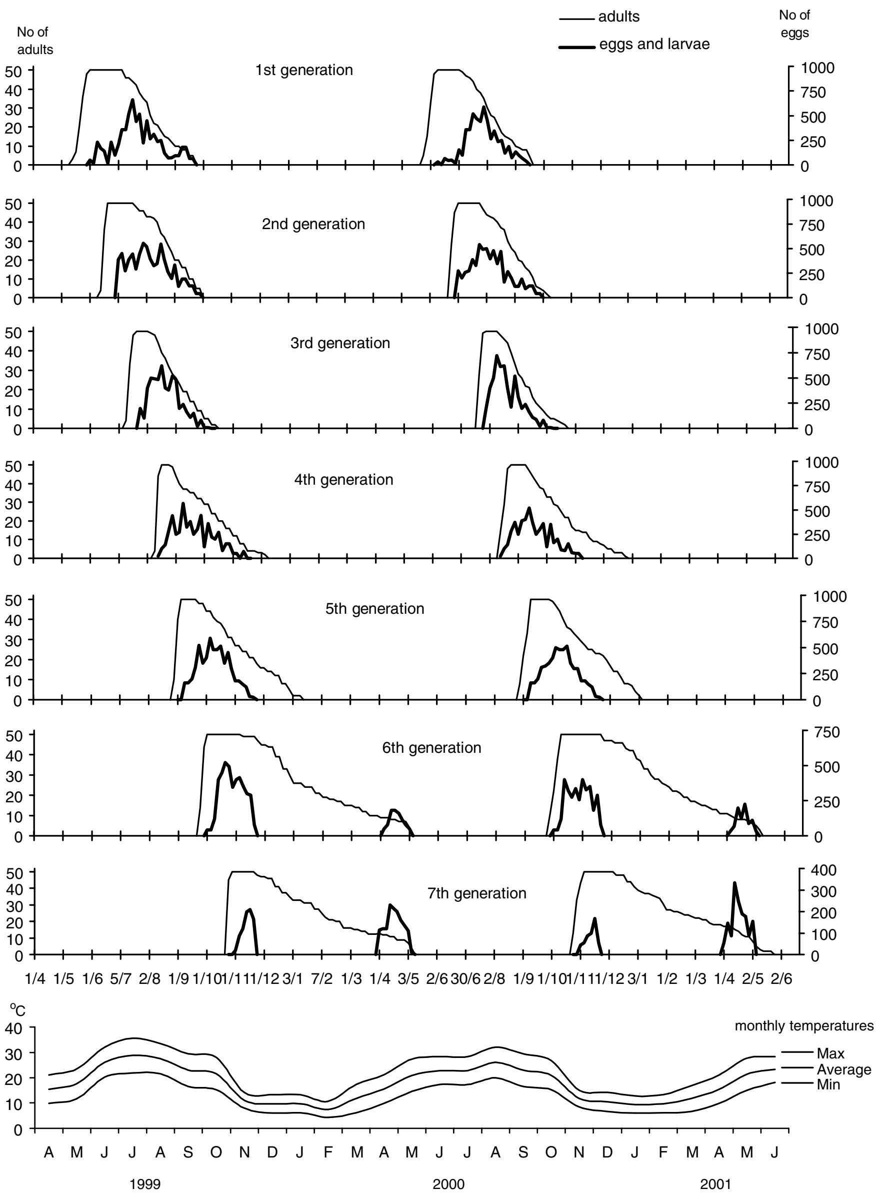

Figure 1. Voltinism, longevity and fecundity of the seven generations of *Hippodamia variegata* adults reared in outdoor cages at Kifissia, Athens in 1999–2001 and monthly temperatures at the same period.

progeny of 6th generation and 26% of the progeny of 7th generation were born before the winter of 2000–2001 and the rest after that. The majority of eggs (87%) were found on squashes, whereas the rest (13%) were laid on cage walls.

Table 1. Mean longevity, average fecundity and sex ratio of the 7 annual generations of *Hippodamia variegata,* in outdoor cages

Generation	Mean longevity (days)		Average fecundity (eggs/female)		Sex ratio (males:females)	
	1999–2000	2000–2001	1999–2000	2000–2001	1999–2000	2000–2001
1st	79 [5][a]	75 [4]	247.6	218.3	1:1.2	1:1.0
2nd	72 [4]	68 [4]	294.4	246.0	1:1.0	1:1.1
3rd	49 [4]	45 [3]	198.2	200.4	1:1.3	1:1.2
4th	55 [5]	59 [6]	195.7	180.6	1:1.3	1:1.3
5th	75 [7]	65 [6]	237.9	204.0	1:1.0	1:1.2
6th	119 [11]	126 [13]	183.5	153.3	1:1.3	1:1.3
7th	112 [10]	122 [12]	82.0	76.3	1:1.2	1:1.1

[a]In brackets are presented the standard errors.

Hippodamia variegata hibernated as adults in small groups. Groups of 2–10 individuals were observed during 29/11/1999–10/3/2000, as well as during 1/12/2000–16/3/2001.

Fecundity (in the laboratory)

The females of *Hippodamia variegata* reared in laboratory conditions started ovipositing 4–7 days after emergence. The daily fecundity and the longevity of the 25 females are presented in Figure 2. The total fecundity ranged between 789 and 1256 and the average total fecundity was 959.6 ± 134.7 eggs.

Most of the eggs were found in clutches of 11–20 eggs (Figure 3). The mean clutch size was 17 eggs and the median clutch size 19 eggs (23,989 eggs have been measured overall).

The summary of the life table of *H. variegata* is presented in Table 2 and the life table parameters are presented in Table 3.

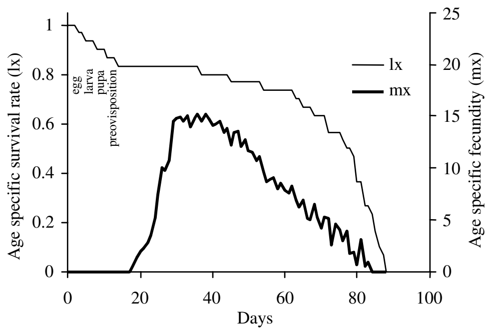

Figure 2. Age specific survival rate (l_x) and age specific fecundity (m_x) of 25 females of *Hippodamia variegata*, in the laboratory.

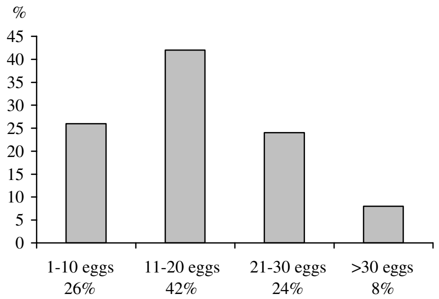

Figure 3. Proportion of eggs of *Hippodamia variegata* in clutches of 1–10, 11–20, 21–30 and >30 eggs, in the laboratory.

Discussion

During the study of the phenology of *H. variegata*, it was ascertained that it completes seven generations in Greece, a number that is high compared to other aphidophagus coccinellid species. *Hippodamia undecimnotata* (Schneider) completes five generations per year, (Katsoyannos et al., 1997a), *Coccinella septempunctata* Linnaeus completes 4 and a 5th partial generation (Katsoyannos et al., 1997b), and *Harmonia axyridis* Pallas 4 generations (Katsoyannos et al., 1997d). Wang et al. (1984) states that *H. variegata* reared on *Schizaphis graminum* (Rondani), *Myzus persicae* (Sulzer) and *Rhopalosiphum maidis* (Fitch) completes three generations per year in China. The difference with the higher number in the present study can be attributed to different climatic conditions of the two areas and different prey. The difference in temperature is the main factor that provides different developmental times. In

Table 2. Summary of the life table of the laboratory population of *Hippodamia variegata*

Observation day	Age specific survival (l_x)	Age specific fecundity (m_x) (15-days sum) (females/female)	Reproductive value (V_x) (females/female)	Excepted remaining life time (E_x) (days)
Immature				
1	1	0	1.2	59.6
15	0.83	0	17.4	59.8
Adult				
30	0.83	84.8	87.4	44.8
45	0.77	215.3	70.0	32.8
60	0.73	157.2	37.3	18.9
75	0.57	83.6	11.4	7.5
83	0.27	15.6	0.9	2.8

Table 3. Life table parameters and stable age distribution of the laboratory population of *Hippodamia variegata*

Life table parameter	Value	Stable age distribution	
		Age	Proportion (%)
R_0	425.9 females/female	Egg	42.1
r_m	0.178 females/female/day	Larva	44.5
T	34.0 days	Pupa	5.6
DT	3.9 days	Adult (1–30 days)	7.6
λ	1.195	Adult (>30 days)	0.2

addition, the kind of prey affects the developmental rate of coccinellids (Hodek, 1973). Furthermore, the geographic variability produces differences in populations of *H. variegata*, such as different developmental rates and longevities (Dobzhansky, 1933).

The increased longevity of hibernating females (6th and 7th generation) compared with that of adults that lived during warmer periods (1st, 2nd and 3rd generation) was caused by low temperatures, and it has been reported for other coccinellids in Greece, as well (Katsoyannos et al., 1997a, b, d; Stathas, 2000a). *Hippodamia variegata* was recorded in the present study to hibernate in groups in the cages. Hodek (1973) states that *H. variegata* hibernates in groups in the field, in contrast with *Coccinella septempunctata* and *Hippodamia undecimnotata* that hibernate in groups on tops of mountains.

Hippodamia variegata females lay eggs for almost all their lifetime (oviposition began 4–7 days after their emergence and stopped 5–7 days before their death), both the laboratory and in the outdoor cages. This fact proves the absence of diapause in *H. variegata* females. This is an important feature of this predator and a major difference from *C. septempunctata* and *H. undecimnotata* that in Greece exhibit summer diapause (Katsoyannos et al., 1997a, b, c). The maximum percentage of the eggs were found in clutches of 11–20 eggs (Figure 3). The mean clutch size was 17 eggs and the median clutch size was 19 eggs. Stewart et al. (1991) report a mean clutch size of 20 eggs. The predator seems to prefer ovipositing on squashes (87% of eggs). This preference of *H. variegata* to lay eggs on a plant surface is also mentioned for *Hippodamia undecimnotata* and *Coccinella septempunctata*, in contrast to other species, which prefer the surfaces of the cages (Hodek and Honek, 1996). It should be mentioned that fecundity calculated in the study of phenology (Table 1) is only a small proportion of the average fecundity that was counted in the laboratory (959.6 eggs per female). These differences could be attributed firstly to lack of food (that was provided twice per week), which could cause a reduction in the egg production. In addition, when the food is limited and the space is prevailing, cannibalism takes place (Hodek, 1973; Hodek and Honek, 1996). It is probable that the high egg density laid per day in the limited space of the cages may have resulted in hatched larvae feeding on the eggs. Furthermore, the extreme upper and lower temperatures in outdoor conditions are additional factors that could reduce the fecundity of *H. variegata*. The reduction is greater in 6th and 7th generation that were affected by winter temperatures.

El Hag and Zaitoon (1996) report smaller values of fecundity, net reproductive value and intrinsic rate of increase of *H. variegata* (fecundity = 276.3 eggs laid per female, $R_0 = 45.6$ females/female, $r_m = 0.082$ females/female/day). The differences with the respective numbers of the present study can be attributed to different conditions and prey (*Brevicoryne brassicae*) that have been used.

From parameter values presented in Table 3, it seems that *H. variegata* is capable of increasing to high numbers in a short time in nature (e.g. the doubling time is less than 4 days). This can also be derived by the results of the study of its phenology in outdoor cages. The stable age distribution shows that the largest proportion (44.5%) of a *H. variegata* exponential increased population constitutes from larvae. This is an advantage because the larva is the most voracious stage in the coccinellids (Hodek, 1973; Stathas, 2000b). The reason that larvae are more multitudinous than the eggs in the stable age distribution is that the larval stage lasts 7–8 days while the egg stage 2–3 days. Releases of large numbers of *H. variegata*, in order to control aphid infestations, can be guided by data from Tables 2 and 3, which can be used to get information about the development of predator population in time; e.g. the highest reproductive value (87.4 females/female) is observed in 30-day old individuals (adults 15 days after their emergence).

The high voltinism of *H. variegata* in Greece (short duration of life cycle), in combination with the reproductive and feeding activity during warm period (absence of summer diapause), result in the development of high populations of the predator in nature (Hodek, 1973; Hodek and Honek, 1996) and prove its effectiveness as a biocontrol agent against aphids in Greece and other parts of the world.

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