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The effect of temperature on the development of the predator *Rhyzobius lophanthae* and its phenology in Greece

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Abstract. The effect of temperature on the development of *Rhyzobius lophanthae* Blaisdell (Coleoptera: Coccinellidae) fed on *Aspidiotus nerii* Bouché (Homoptera: Diaspididae) under controlled laboratory conditions was studied. The duration of each developmental stage and adult longevity were measured at 15, 20, 25, and 30 °C. The life cycle of *R. lophanthae* (from egg to oviposition) lasted 78.7, 43.6, 32.1, and 23.9 days, whereas the average adult longevity was 257.6, 171.4, 121.3, and 88.5 days at each temperature, respectively. Low temperature thresholds of *R. lophanthae* immature life stages ranged from 7.6 to 9.3 °C, while the thermal constant for the development of *R. lophanthae* from egg to adult was 443.5 degree-days. The average fecundity at 25 °C was 633.7 eggs per female. *Rhyzobius lophanthae* reared in cages outdoors during 1993–1995 at Kifissia, Athens developed 5 complete overlapping generations per year from May to October and a 6th partial overlapping generation during February and March. Adults of the 4th and 5th generation survived winter conditions giving rise to the following year's 1st generation. Females were reproductively active throughout the year, indicating that *R. lophanthae* does not diapause.

Key words: fecundity, phenology, rearing, temperature threshold, thermal constant, Coccinellidae, Coleoptera, *Aspidiotus nerii*, *Rhyzobius lophanthae*

Introduction

The Australian native coccoidophagous predator, *Rhyzobius lophanthae* Blaisdell (Coleoptera: Coccinellidae), has been reported as an important natural enemy of most armored scale species of the family Diaspididae (Homoptera: Coccoidea) (Hodek, 1973; Rosen, 1990). It has successfully been introduced to many countries including California (Yus, 1973), Italy (Bouvier, 1913; Smirnoff, 1950), Argentina (Salvadores, 1913), Bermuda (Bennet and Hughes, 1959), Algeria, Tunisia, Morocco (Rungs, 1950; Smirnoff, 1950), and Georgia (Rubstov, 1952) for the control of armored scales. In Greece, although there are no reports on its introduction, *R. lophan-*

thae was first recorded in 1960 in Peloponnese and in Central and Northern Greece on olive trees harboring armored scales (Argyriou and Katsoyannos, 1977).

Very little is known about the effect of temperature on the development of *R. lophanthae* or about its phenology. Smirnoff (1950) reported that the *R. lophanthae* life cycle, egg development, 1st and 2nd instars, 3rd and 4th instars, and pupal development lasted about 27–30, 6, 9, 5–6, and 7–8 days, respectively, at temperatures ranging from 20 to 25 °C and relative humidity from 60 to 80%. However, duration of each larval stage separately, the thermal thresholds, as well as the conditions of rearing (photoperiod and host) were not mentioned. Cividanes and Gutierrez (1996), describing a model for *R. lophanthae* development focussed on the relationship between daily prey consumption and fecundity. Field observations on populations of *R. lophanthae* showed that the species does not seem to diapause (Smirnoff, 1950; Rubstov, 1952). Rubstov (1952) observed larval stages during winter. Smirnoff (1950), although he does not refer to results of *R. lophanthae* rearing on a specific host scale species, supposes that it may be able to reach a maximum of 7–8 generations per year in Morocco and indicates the need for further investigation of voltinism.

This study was conducted to determine the effect of temperature on the duration of stage development and on adult longevity of *R. lophanthae* as well as the low temperature thresholds, thermal constants, and regression lines (developmental rate in relation to temperature) for each immature stage. Since there are no reports on *R. lophanthae* phenology, except for a few data from observations on natural populations, the species phenology was also studied. Studies were conducted to determine the number of generations per year, adult longevity in each generation, and immature stage development during the winter. Finally, to determine whether there was summer and winter diapause, the reproductive activity of females reared in outdoor cages was studied throughout a year.

Materials and methods

The initial population of *R. lophanthae* originated from Leonidion, Peloponnese, Greece. Adults and larvae were collected from lemon and sour orange trees infected by the scale *Parlatoria pergandei* Comstock (Homoptera: Diaspididae), on 19 April 1993 and were transferred to the Benaki Phytopathological Institute. *Rhyzobius lophanthae* colonies were reared in cylindrical plexiglass cages (30 cm in diameter, 50 cm in length) (Iperti and Burn, 1969), on the scale *Aspidiotus nerii* Bouché (Homoptera: Diaspididae). *Aspidiotus nerii* was reared in the laboratory on fruits of

Cucurbita maxima Duchesne (Cucurbitaceae), potato tubers, and potato sprouts.

Laboratory experiments

The effect of temperature on the development of *R. lophanthae* was studied at 15 ± 1, 20 ± 1, 25 ± 1, and 30 ± 1 °C. The relative humidity was 65% with a 16:8 (L:D) photoperiod at all four temperatures. This long photoperiod is recommended for the study of the biological characteristics of coccinellids and has been used previously in similar studies (Baumgartner et al., 1987; Cividanes and Gutierrez, 1996; Katsoyannos et al., 1997 a and b). The length of egg, larval, and pupal stages, the preoviposition period, and adult longevity were measured under these conditions. Data were taken from 25 individuals in each case, except for the study on the duration of the preoviposition period, which was carried out on 13 females at 15 °C and 25 °C and on 14 females at 20 °C and 30 °C. Each individual was reared separately in a Petri dish (9 cm diameter). Measurements were recorded once a day. Insects were fed on nymphs of *A. nerii* infesting potato sprouts. The potato sprouts were chosen because of their convenient shape and size for the Petri dishes used.

The thermal summation method was used to estimate the thermal constant (K). The constant is the number of degree-days required to complete the development of one stage according to the formula K = D (T-t), where D = days for development at temperature T and t = the developmental threshold. The developmental threshold is the lowest temperature at which development occurs. The developmental thresholds and thermal constants were calculated for each immature stage. For each stage of development, the regression equation y = a + bT (where y = 1/D) and the coefficients of determination R^2 are given. The point of interception of the regression line with the X axis corresponds to the threshold temperature t. The thermal constant, K, is determined as 1/b (Wigglesworth, 1953; Campbell et al., 1974; Johnson et al., 1979).

To estimate the average fecundity, 25 females were reared in male-female pairs in cylindrical glass cages (16 cm in diameter × 25 cm in length) at 25 ± 1 °C, ∼65% relative humidity, and 16:8 (L:D) photoperiod. Inside these cages, the adults were fed on nymphs of *A. nerii* on potato sprouts. Potato sprouts were used because their shape enabled their examination under the stereo-microscope in order to determine the number of *R. lophanthae* eggs.

Outdoor experiments

To study *R. lophanthae* phenology, adults from 60 larvae collected from the field were used to initiate the first generation. Larvae were reared together in a cylindrical plexiglass cage (30 cm in diameter, 50 cm in length) placed outdoors near the laboratory of Benaki Phytopathological Institute, Kifissia, Athens. Successive generations were separated from one another by moving the first 60 neonates from each generation into a new cage. The rest of the larvae were counted and then were removed from the cages. This was repeated until all adults that started each generation had died. The number of living adults, larvae, and matings in each cage was recorded twice per week. Larvae were fed with nymphs of *A. nerii* reared on fruits of *Cucurbita maxima*, potato tubers, and sprouts. In this case, we used *C. maxima* fruit and potato tubers because they remain fresh inside the outdoor cages for a longer period of time (several months) compared to potato sprouts (15–20 days).

To calculate the percentage of females of *R. lophanthae* that were actively reproductive in each generation, 25 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. After oviposition had begun, the adults of each generation (males and females) were transferred to a cylindrical plexiglass cage (30 cm × 50 cm). Measurements (number of eggs) were taken every second day.

The ability of *R. lophanthae* to oviposit during the winter was studied from October 1993 to March 1994 and from October 1994 to March 1995. During these periods, *C. maxima* fruit and potatoes infested by *A. nerii* were placed inside the cages to feed the adults. Plant material was replaced every 15 days and removed material was placed in separate cages until hatching was observed. In this way, the time when the eggs were laid and the time of hatching were determined. *Cucurbita maxima* fruit and potatoes were used because of their ability to remain fresh in outdoor cages for a long period of time (from the laying of eggs until the hatching of larvae).

The maximum and minimum temperatures were recorded daily at Benaki Phytopathological Institute. These were used to calculate the daily degree-day accumulation using $[(Tmax + Tmin)/2] - t$ when $Tmin > t$ and $[(Tmax + t)/2] - t$ when $Tmin < t$ (Wright and Laing, 1978). The degree-days accumulated was calculated from the date of 50% adult emergence (30 out of 60 beetles) of one generation until the date of 50% adult emergence of the next generation. (Wright and Laing, 1978; Johnson et al., 1979).

Results

Laboratory experiments

Effect of temperature

The duration of egg development was longer than the duration of the other stages, at all temperatures (Table 1). The duration of the 4th instar was the second longest followed by the duration of the pupae, the preoviposition period, and the 1st, 3rd, and 2nd instars at all temperatures. The temperature threshold fluctuated between 7.6 °C (for the 3rd instar) and 9.3 °C (for the 1st instar). All larvae survived to adults at all temperatures. The linear regression parameters (intercept and slopes) describe the relationship between developmental rate (y) and temperature (x) (Table 1). The smallest slope (0.0086) was observed at the egg stage which had the longest duration at all temperatures. For the rest of the stages, the slope increased as the duration of development decreased, reaching the highest value for the 2nd instar (0.0288). The coefficient of determination (R^2) ranged from 0.9816 (3rd instar) to 0.9968 (eggs) indicating a good linear relationship for all developmental stages.

Adult longevity decreased with increasing temperature (Figure 1). The average adult longevity (mean ± SD) was 257.6 ± 50.13 days at 15 °C, 171.4 ± 49.41 days at 20 °C, 121.3 ± 31.85 days at 25 °C, and 88.5 ± 40.70 days at 30 °C.

Fecundity

The average fecundity of females reared in pairs at 25 °C was 633.7 (SD:199.7) eggs per female, and the average longevity of the females was 63.4 (SD:19.8) days. The female fecundity ranged from 222 eggs laid by a female that lived 17 days, to 1152 eggs laid by a female that lived 110 days.

Outdoor experiments

Voltinism

Rhyzobius lophanthae developed 6 generations from May 1993 to March 1994 and from May 1994 to March 1995 (Figure 2). Among the first 60 hatched larvae of each generation that developed to adults of the next generation, mortality was observed only in the progeny of the 5th generation in both years studied. In March 1994, 32 of them developed to adults of the 6th generation (53.3%), 12 died at the 4th instar (20%) and 16 died at the pupal stage (26.7%). In March 1995, 22 larvae developed to adults of the 6th generation (36.7%), while 17 died at the 4th instar (28.3%) and 21 at the pupal stage (35%).

Table 1. Development of *Rhyzobius lophanthae* under constant temperatures

Stage	Temperature				t (°C)	K	Regression lines	R^2
	15 °C	20 °C	25 °C	30 °C				
Egg								
D	17.2	10.1	7.4	5.2	8.2	116.3	y = 0.0086x – 0.071	0.9968
S.D.	0.85	0.81	0.51	0.37				
(n=25)								
First instar								
D	8	4.8	3	2.4	9.3	49	y = 0.0204x – 0.189	0.9966
S.D.	0.45	0.76	0.45	0.50				
(n=25)								
Second instar								
D	5.4	3	2.2	1.6	8.6	34.7	y = 0.0288x – 0.248	0.9931
S.D.	0.77	0.20	0.37	0.49				
(n=25)								
Third instar								
D	5.5	3.6	2.7	1.9	7.6	43.9	y = 0.0228x – 0.173	0.9816
S.D.	0.51	0.50	0.61	0.33				
(n=25)								
Fourth instar								
D	15.4	8.1	6.2	4.9	7.8	108.7	y = 0.0092x – 0.072	0.9888
S.D.	1.8	0.66	0.50	0.67				
(n=25)								
Pupa								
D	13.9	7.2	5.6	4.1	8.2	90.9	y = 0.011x – 0.09	0.9902
S.D.	0.81	0.37	0.51	0.33				
(n=25)								
Preoviposition period								
D	13.2	6.8	5	3.8	8.8	80.6	y = 0.012x – 0.109	0.9907
S.D.	2.95	0.58	0.85	0.97				
	(n=13)	(n=14)	(n=13)	(n=14)				
Total development of life cycle								
D	79	43.4	32	23.9	8.4	526.3	y = 0.0019x – 0.0159	0.9977
S.D.	3.08	1.34	1.21	1.00				
	(n=13	(n=14)	(n=13)	(n=14)				

(D: days, S.D.: Standard Deviation, n: number of individuals, t: temperature threshold, K: thermal constant, y = developmental rate, x = temperature, R^2: coefficient of determination).

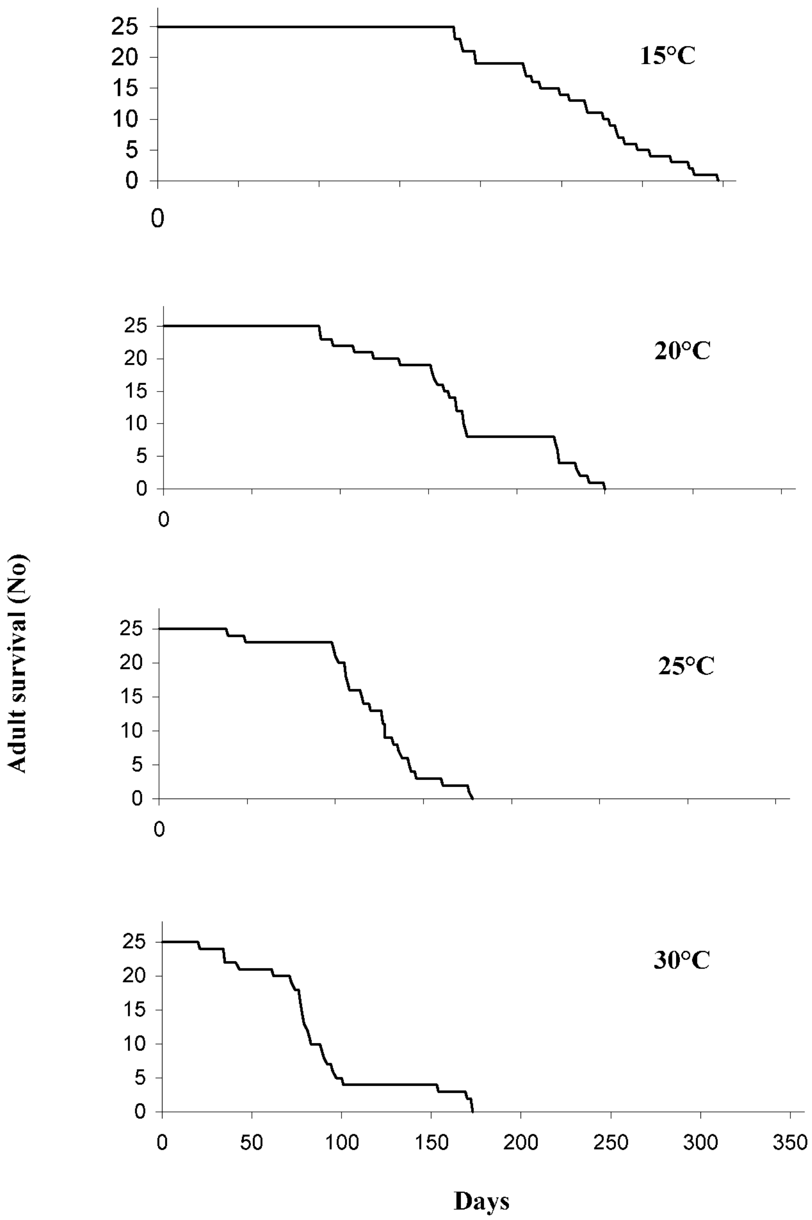

Figure 1. Adult longevity of *Phyzobius lophanthae* under constant temperatures.

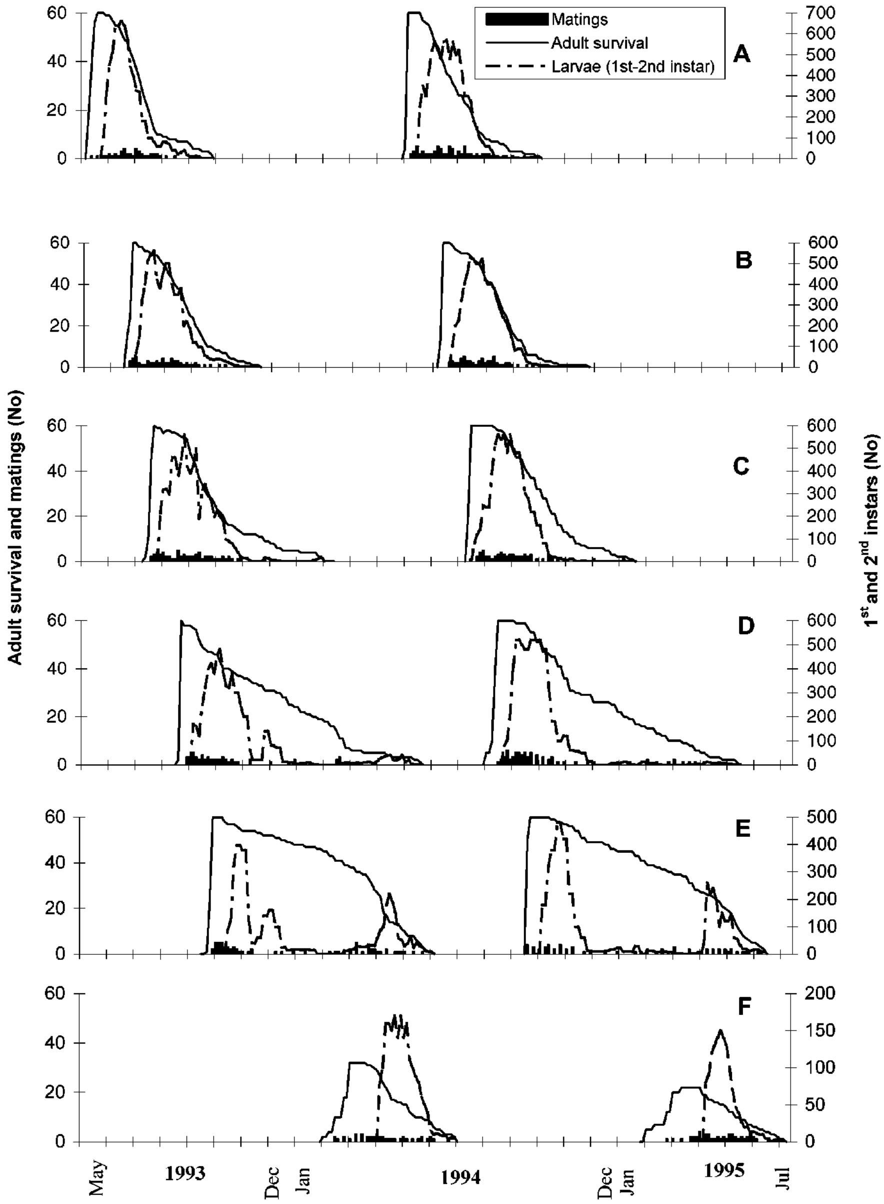

Figure 2. Voltinism, adult longevity and larval production of 60 *Rhyzobius lophanthae* adults reared in outdoor cages at Kiffissia, Athens in 1993–1995 (A. B. C. D. E. F: 1st, 2nd, 3rd, 4th, 5th and 6th generation, respectively).

The degree-days that accumulated during the time periods between successive generations of *R. lophanthae* in outdoor cages ranged between 513.9 and 571.2 degree-days.

Adult longevity

The adults of the first generation lived until October in both years (1993–1994 and 1994–1995) (Figure 2). The adults of the 2nd and 3rd generation died during winter (November–February) whereas the adults of the 4th, 5th and 6th generation survived winter conditions and lived until the following summer (June–July).

Reproductive activity

The number of matings shown in Figure 2 do not correspond to the total 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 the adult longevity in all generations.

By rearing 25 females from each generation in a separate cage, it was possible to observe that the females of all generations oviposited. In the 1st year (1993–1994) the average larval production of *R. lophanthae* females from 1st to 6th generation was 212.6, 190.9, 236.6, 183.3, 129.3, and 113.0, larvae per female respectively, while during the 2nd year (1994–1995) it was 213.7, 204.7, 205.5, 143.4, 116.1 and 114.6 larvae per female respectively.

The largest number of progeny of *R. lophanthae* (1st and 2nd instars) were observed from June to November for both years in outdoor cages (Figure 2). The females of the 1st and 2nd generation produced all their progeny during this period, while females of the 3rd, 4th, and 5th generations produced the maximum number of progeny. Few progeny were observed between December and March when the adults of the 3rd, 4th, and 5th generation produced a small percentage of their progeny. An increase in the number of progeny per female in the 5th generation and in the total number of progeny per female in the 6th generation was observed from April to July of the following year. Egg laying activity was observed during the winter (October–March), except for the first half of February and the second half of January in years 1994 and 1995.

Discussion

Effect of temperature

There is little information available on the effect of temperature on the development of *R. lophanthae*. Smirnoff (1950) gave some data on the duration of development of *R. lophanthae* (see introduction section) which cannot be directly compared to the findings of the present study because of the variable rearing conditions under which his study was carried out. Cividanes and Gutierrez (1996) reported that the required temperature thresholds for development from egg to pupa and from pupa to adult were 8.5 and 10.3 °C, respectively, when *R. lophanthae* was reared on *A. nerii*. Their value of temperature threshold required for development from egg to pupa is close to the average temperature threshold found in the present study for the respective stages (8.4 °C). In contrast, the temperature threshold they reported for the development of the pupa differs from the respective temperature threshold found in the present study (8.2 °C). The difference may be attributed to the fact that in the study of Cividanes and Gutierrez the relative humidity was not controlled but generally varied between 50–70%.

Adult longevity

The average longevity of adults reared individually at 25 °C (121.3 days) (Figure 1) was longer than that of adults reared in pairs (one male with one female in each cage in the study of fecundity) at the same temperature (63.4 days). The difference could be attributed to their mating activity, a phenomenon that has been observed in other insects (Lingren et al., 1988; Quiring and McNeil, 1984). The adult longevity in outdoor cages ranged from 4 to 9 months. The long adult lifespan in the 4th and 5th generations (those that survived winter conditions) could be attributed to the decrease in adult activity caused by winter temperatures.

Reproductive activity

In the present study the observed fecundity of *R. lophanthae* is considerably higher than for other coccoidophagous predators (Rosen, 1990). The average number of larvae produced per female of *R. lophanthae* in each generation (during summer and winter months in outdoor cages), ranged from 113 to 236.6 eggs. The fecundity observed in outdoor cages was about 1/3 of the average fecundity that was counted in the laboratory (633.7 eggs). The difference could be attributed to cannibalism which takes place when conditions of lack of food and space are prevailing (Hodek, 1973). 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. The reduction in the number of matings that was observed during winter months for adults that overwintered could be simply explained by the decrease in temperature. The relatively small number of progeny that was produced by the females of the 4th, 5th, and 6th generation could be explained by egg mortality or temper-

Table 2. Degree-day accumulation from May 1993 to March 1995, for *Rhyzobius lophanthae* reared in outdoor cages, at Kifissia, Athens

Degree-day accumulation between successive generations		
Period	Generations	Degree-days
24/05/93 – 02/07/93	1st – 2nd	540.5
03/07/93 – 29/07/93	2nd – 3rd	513.9
30/07/93 – 29/08/93	3rd – 4th	559.7
30/08/93 – 05/10/93	4th – 5th	529.9
06/10/93 – 10/03/94	5th – 6th	558.4
11/03/94 – 22/05/94	6th – 1st	524.9
23/05/94 – 29/06/94	1st – 2nd	535.1
30/06/94 – 02/08/94	2nd – 3rd	547.3
03/08/94 – 28/08/94	3rd – 4th	518.2
29/08/94 – 02/10/94	4th – 5th	541.5
03/10/94 – 11/03/95	5th – 6th	571.2

atures below developmental threshold. The mating and oviposition observed suggested that *R. lophanthae* has no diapause. The absence of diapause, as well as the presence of larvae during the winter period have been reported for *R. lophanthae* in other regions such as Morocco (Smirnoff, 1950) and Georgia (Rubstov, 1952).

Voltinism

Smirnoff (1950), supposes that *R. lophanthae* may be able to reach a maxium of 7–8 generations per year in Morocco. As it is recorded in the present study, *R. lophanthae* completes 6 generations per year in Greece. In either case, the number of generations completed per year is higher than that completed by other coccoidophagous predator species. Other predators of diaspidids, like *Chilocorus bipustulatus* Linnaeus (Coleoptera: Coccinellidae) (Bodenheimer, 1951) and *Cybocephalus fodori* Endrödy-Younga (Coleoptera: Nitidulidae) (Katsoyannos, 1984) complete 3 generations per year. The rapid population development of *R. lophanthae* (1 generation per month during the warm period of the year) makes it a very effective biological control agent against diaspidids (Hodek, 1973; Rosen, 1990).

The degree-days accumulated during the periods between successive generations of *R. lophanthae* when reared outdoors (Table 2) fluctuated around the value of the thermal constant estimated for the completion of the life cycle of *R. lophanthae* (526.3 degree-days, Table 1). The greatest differences from this value were observed for the periods between the 5th and 6th generation (from October 1993 to March 1994: difference = 32.1 degree-days and from October 1994 to March 1995: difference = 44.9 degree-days). These differences could be explained by the high mortality of the 5th generation progeny, which subsequently led to a delay in the completion of the 6th generation in both years (1994 and 1995).

Rhyzobius lophanthae appears to possess favorable biological and ecological traits to make it an effective biological control agent against diaspidids. The ability of larvae to develop even during winter, the lack of diapause, and the short life cycle may contribute to a great population increase rate in nature. Furthemore, data on factors like voltinism, rate of development, fecundity and longevity may be used in indirect evaluation of the effectiveness of Coccinellidae (Hodek, 1973).

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