THERMAL REQUIREMENTS FOR DEVELOPMENT OF *COLEOMEGILLA MACULATA* (COLEOPTERA: COCCINELLIDAE) AND ITS PARASITE *PERILITUS COCCINELLAE* (HYMENOPTERA: BRACONIDAE)

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Abstract

Can. Ent. 110: 407–412 (1978)

The optimum temperature range for development and survival of the predacious coccinellid *Coleomegilla maculata* and its parasite *Perilitus coccinellae* is 24° to 26.7°C. Theoretical thresholds for development (*t*) of the pre-imaginal stages of *C. maculata* range from 9° to 13°C. Total development (from oviposition to adult emergence) of the beetle requires an accumulation of 236 heat degree days (*K*) above 11.3°C (*t*), whereas the development of *P. coccinellae* requires 395 heat degree days (*K*) above 9.8°C (*t*). To predict the seasonal interaction between *C. maculata* and *P. coccinellae*, and to manage *C. maculata* efficiently as a biological control agent, it is vital to know the thermal and dietary requirements of the two species.

Introduction

Coleomegilla maculata (De Geer) is a native beneficial coccinellid that is widely distributed east of the Rocky Mountains in North America. It is common in fields of alfalfa, corn, and turnips (Richerson and DeLoach 1973), and it is considered an important predator of numerous insect pests, including the cereal leaf beetle (Shade *et al.* 1970), the bollworm (Whitcomb 1967), and the European corn borer (Whitman 1975).

In turn, *C. maculata* is attacked in the adult stage by *Perilitus coccinellae* (Shrank), a thelyotokous parasite of several coccinellid species (Hodek 1973). Some authors have assumed that *P. coccinellae* reduces the effectiveness of this predator as a biological control agent (Balduf 1926; Richerson and DeLoach 1973). However, this assumption is open to question because it has not been tested and also because the analogous problem of the impact of hyperparasites on the population dynamics of primary parasites and their hosts is an unresolved question that is now being re-examined (Huffaker *et al.* 1977). Therefore, to increase the potential usefulness of *C. maculata* as a biological control agent, we initiated a study of its interaction with its parasite *P. coccinellae*. This paper presents the stage-specific thermal requirements for development of both species.

Materials and Methods

C. maculata

Adults of *C. maculata* (*lengi* variety) from Ithaca, N.Y., were maintained at L:D 16:8, 24±1°C, and were constantly provisioned with water, a Wheast®-protein food mixture, *Acyrthosiphon pisum* (Harris) (pea aphids), and *Myzus persicae* (Sulzer) (green peach aphids). Egg clusters from each fertile female were distributed among five constant temperature conditions (Table I). On the day of hatching we transferred each first instar larva to a separate vial. Larvae were given *M. persicae* that had been reared on Chinese cabbage, *Brassica oleracea* L. There were three replicates for each temperature; each replicate consisted of 20 to 36 individuals. All tests used the first generation offspring of field-collected adults.

The larvae were examined daily; developmental time was recorded for each pre-imaginal life stage (ecdysis to ecdysis) and also for the total life cycle. The fourth instar included the "prepupa", an immobile stage preceding the pupal ecdysis.

Table I. Development and mortality of *Coleomegilla maculata* under various temperatures, ± 1°C (L:D 16:8)

	Developmental times (days; mean of replicate means ± S.E.)				
	18.3°	21.1°	24.0°	26.7°	29.4°
Egg	5.44±.26	4.21±.18	3.22±.08	2.72±.50	2.18±.20
1st instar	5.39±.16	3.31±.27	3.10±.14	2.36±.48	2.12±.10
2nd instar	3.59±.22	2.63±.02	2.02±.21	1.55±.33	1.28±.12
3rd instar	4.12±.35	2.98±.30	2.54±.07	1.83±.09	1.71±.04
4th instar and prepupa	8.23±.29	5.62±.23	4.81±.27	4.11±.24	2.88±.07
Pupa	6.70±.24	4.96±.001	3.66±.31	2.89±.25	2.76±.15
Total development	33.45±.91	23.72±.79	19.34±.51	15.40±.31	12.93±.19
	% mortality (mean of replicate percentages ± S.D.)				
	6±3	20±6	16±9	24±18	27±19
No. in each replicate	(32,32,29)	(27,27,26)	(20,27,36)	(24,27,23)	(24,24,28)

P. coccinellae

P. coccinellae females were obtained from field-collected *C. maculata* hosts. They were maintained at L:D 16:8, 24±1°C, in cages provided with water, honey, a Wheast®-protein food mixture, and honeydew. The first laboratory generation adults of *C. maculata* served as hosts for the *P. coccinellae*. All host beetles were given a daily supply of pea aphids and green peach aphids. We exposed groups of four or five *C. maculata* adults to pairs of *P. coccinellae* females for 8 h. These beetles were then distributed among five constant temperature conditions (Table III). We recorded the parasite egg–larval developmental time (days from host exposure to parasite emergence and cocoon formation), prepupal–pupal development time (days from cocoon formation to adult emergence), and adult longevity (days from emergence to death). For the tests of adult longevity, parasites were provided with water, honey, a Wheast®-protein food mixture, and honeydew.

Statistical Analysis

The reciprocal of the mean developmental time (1/days) was plotted against temperature and the resulting curve was tested for linearity using the ANOVA test (Snedecor and Cochran 1967). The theoretical threshold for development (t) was estimated by extrapolation, and the thermal constant (K) was then calculated from the equation $K = y(d-t)$, where y = mean developmental time (days), d = temperature (°C), t = theoretical threshold for development (°C) (Andrewartha and Birch 1954; Wigglesworth 1972). We calculated standard errors for each t and K value following a method outlined by Campbell *et al.* (1974), but which was modified for replicated data (Tauber *et al.*, in prep.).

Results

C. maculata Development

Both the developmental rates and the mortality of *C. maculata* increased with increasing temperature (Table I). Between 18.3° and 29.4°C, the ANOVA test showed that the rate of development of each life stage (except the fourth instar–prepupa) and the total life cycle (Table I) had a linear relationship with temperature (level of significance = 0.05). For the fourth instar–prepupal stage, temperature and rate of development had a linear relationship over the range of 18.3° to 26.7°C.

All *t* values fell between 9° and 13°C, and the *K* value for the total life cycle was 236 heat degree days above 11.3°C (Table II). Fourth instar larvae had the lowest *t* value (9.4°C), the largest *K* value (70), and it represents the greatest percentage of the total life cycle at all temperatures (approx. 25%). The second instar had the highest *t* value (12.7°C), the lowest requirement of heat degree days (22), and the smallest percentage (10%) of the total life cycle (Table II).

Parasite Development

Between 15.6° and 26.7°C the developmental rates (Table III) of *P. coccinellae* showed a linear relationship with temperature (level of significance = 0.05). The *t* values for *P. coccinellae*'s three developmental periods were approximately 10°C; the *K* value for the total life cycle was 395 heat degree days above 9.8°C (Table II). Mean adult longevity increased from 4 to 8 days at lower temperatures (Table III).

Parasite survival (as measured by adult emergence) was greatest at 24°C, and it decreased progressively with decreasing temperatures (Table III). Mean survival of parasite pupae showed a similar trend.

Incidence of host mortality (without parasite emergence) was highest at 15.6° and 18.3°C and lowest at 26.7°C. The dead beetles had a high incidence of superparasitism (75%, $N = 12$).

Discussion

Optimum Temperatures

Based on developmental rates and mortality, we conclude that *C. maculata's* optimum temperature falls between 24° and 26.7°C. Although the developmental rate at 26.7°C was faster than at 24°C, the mortality at 26.7°C was also consistently but not significantly higher. These observations are consistent with the results obtained by Smith and Williams (1976), who reported that the fecundity of *C. maculata lengi* was highest at 25°C, fertility greatest at 23° to 25°C, and longevity for laboratory-reared adults longest at 23°C.

P. coccinellae's optimal temperature was similar to its host's. The low parasite survival at 15.6° and 18.3°C was correlated with both low host survival and low survival of the parasite pupae at these temperatures (Table III).

In an earlier study Gurney and Hussey (1970) reared *C. maculata* from Trinidad at three temperatures (16°C, 21°C, 24°C). Using their data we calculated the *t* and *K* values for the total life cycle; they are 10.9°C and 262 heat degree days, respectively. These values were not greatly different from the values of 11.3°C and 256 heat degree days that we obtained from the Ithaca population (Table II). Similarly, in their studies using fluctuating temperatures ($\bar{x} = 26.1$°C), Simpson and Burkhardt (1960) reported that

Table II. Developmental thresholds (*t*) and thermal constants (*K*) for *Coleomegilla maculata* and *Perilitus coccinellae* ($\bar{x}$ ± S.E.)

	t (°C)	*K*		*t* (°C)	*K*
C. maculata			***P. coccinellae***		
Egg	11.3±0.9	40.2±1.8	Egg–larva	9.9±0.2	275.7± 2.9
1st instar	10.4±2.5	39.8±4.8	Pupa	10.0±0.7	120.2± 4.1
2nd instar	12.7±0.9	21.6±1.1	Total development	9.8±0.6	395.0±11.8
3rd instar	10.8±2.1	31.3±3.1			
4th instar and prepupa	9.4±1.8	69.9±7.5			
Pupa	10.2±1.1	48.8±4.9			
Total development	11.3±0.6	235.8±0.7			

Table III. Development, longevity, and survival of *Perilitus coccinellae*; and survival of *Coleomegilla maculata* adults under various temperatures, ± 1°C (L:D 16:8)

	Developmental times (days; mean of replicate means ± S.E.)				
	15.6°	18.3°	21.1°	24°	26.7°
Egg–larva	47.9±5.0 (6,5,12)[a]	33.2±2.1 (9,10,14)	24.7±0.6 (13,15,15)	19.7±0.9 (18,11,17)	16.3±0.3 (15,12,20)
Pupa	20.8±0.7 (3,3,10)	15.0±1.6 (5,6,12)	10.8±0.1 (9,13,11)	8.8±0.3 (15,10,16)	7.1±0.3 (11,6,18)
Total development	65.8±3.0 (3,3,10)	48.4±3.8 (5,6,12)	34.6±0.8 (9,13,11)	28.0±0.9 (15,10,16)	23.3±0.2 (11,6,18)
	Parasite adult longevity (days; mean of replicate means ± S.E.)				
	8.4±3.6 (3,3,10)	7.2±1.9 (5,6,12)	6.9±1.8 (9,13,11)	5.9±0.6 (15,10,16)	4.2±1.1 (11,6,18)
	% survival until parasite emergence (mean of replicate percentages ± S.D.)				
C. maculata					
exposed to parasites	45± 6	52± 6	71± 7	74±10	79±10
unexposed to parasites	74± 7	81±20	94±10	93±11	94±10
P. coccinellae					
Pupal[b]	64±17	67±16	76± 9	89± 6	71±20
Total[c]	22±13	32±11	47± 7	56±13	50±22

[a] No. of individuals in each replicate.

[b] (No. of emerging adults/No. of pupae) = pupal survival.

[c] (No. of emerging adults/No. of hosts exposed to parasites).

total development (from oviposition to adult) for *C. maculata* ranged from 15 to 19 days ($\bar{x} = 17.4$). The pre-imaginal developmental times as well as total development reported in their study closely agreed with the values we observed at a constant 26.7°C (Table I).

The egg–larval developmental time (24.7 days at 21.1°C) that we recorded for the parasite *P. coccinellae* in *C. maculata*, is similar to that previously reported by Balduf (1926) for the same two species; but it is much longer than the period (13–14 days at 70±5°F) given by Sluss (1968) for *P. coccinellae* in *Hippodamia convergens* males. This difference in parasite developmental time may result from (*a*) differences in host suitability, (*b*) microsporidian infections observed by Sluss (1968) in both the parasite and its host, or (*c*) differences in *P. coccinellae* strains.

Parasite pupal developmental times that we obtained at 21.1°C (Table III) closely agree with the value previously reported by Smith (1960). Also, our adult longevity data are not greatly different from the values given by Balduf (1926) for *P. coccinellae* on a honey diet, or by Smith (1960) (parasite diet not given); both investigators worked with *P. coccinellae* reared from *C. maculata*. Iperti (1964) observed similar periods of adult longevity (3 to 11 days) at 20° to 25°C, but much longer adult life at 14°C for *P. coccinellae* from *Coccinella septempunctata* L. (diet not given).

Seasonal Activity

Knowledge of thermal requirements for development is important in predicting the seasonal timing of host–parasite interactions. For example, despite the problems inherent in extrapolating laboratory results to the field, the thermal data we obtained for

C. maculata and *P. coccinellae* are useful in estimating the maximum number of generations possible in a year. Thus, we predict that early in the spring, when temperatures are close to the developmental thresholds, the slightly lower *t* values characteristic of *P. coccinellae* allow it to begin development prior to its host. The lower *t* values would not substantially alter the developmental time relative to its host later in the season when temperatures are high (see Campbell *et al.* 1974; Tauber and Tauber 1976). The much higher *K* values for *P. coccinellae* indicate that at high temperatures its development would take longer than *C. maculata*'s. Therefore, based solely on thermal requirements, *C. maculata* would be expected to produce more generations per year than *P. coccinellae*. This conclusion differs with observations that *P. coccinellae* produces 4 or 5 generations per year (Balduf 1926; Richerson and DeLoach 1973) and that *C. maculata* produces 2 or 3 generations per year (Pack 1925; Putman 1964). We propose that other environmental factors, e.g. differences in time of diapause induction and termination, and quality and quantity of food, may be as important as temperature in determining the number of generations of the beetle and its parasite.

C. maculata is polyphagous (Hodek 1973), and the quantity and quality of its food can strongly influence its development. Previous studies have shown that (1) development was slightly slower when larvae fed on the mite *Tetranychus telarius* than when they fed on *Rhapalosiphum rufomaculatum,* an aphid (Putman 1957), (2) the rate of development decreased as a result of food shortage (Smith 1965*a*), (3) individuals completed development on a variety of plant pollens (Smith 1961), but (4) development was more rapid and survival higher when *C. maculata* was reared on a mixture of corn aphids and corn pollen than when larvae received either food alone (Smith 1965*b*). Thus, both the type and amount of food can greatly affect the number of generations that *C. maculata* has per year. Given that prevailing temperature conditions in eastern North America are sufficient to allow more than the observed 2 to 3 generations per year, we suggest that *C. maculata*'s rate of development could be increased by provisioning selected sites with an appropriate synthetic diet as has been proposed for other entomophagous species (see Hagen *et al.* 1971 and van den Bosch and Messenger 1973). In this way the effectiveness of *C. maculata* as a biological control agent could be increased.

Acknowledgments

We thank the following collectors of living specimens: Catherine, Paul, Michael and Agatha Tauber. We thank C. L. Wood, Cornell University, for assistance with statistical procedures, and J. R. Nechols, Cornell University, for technical help.

References

Andrewartha, H. G. and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press.

Balduf, W. V. 1926. The bionomics of *Dinocampus coccinellae* Shrank. *Ann. ent. Soc. Am.* **19**: 465–489.

Campbell, A., B. D. Frazer, N. Gilbert, A. P. Gutierrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. *J. appl. Ecol.* **11**: 431–438.

Gurney, B. and N. W. Hussey. 1970. Evaluation of some coccinellid species for the biological control of aphids in protected cropping. *Ann. appl. Biol.* **65**: 451–458.

Hagen, K. S., E. F. Sawall, Jr., and R. L. Tassan. 1971. The use of food sprays to increase effectiveness of entomophagous insects. *Proc. Tall Timbers Conf.* on Ecological Animal Control by Habitat Management **2**: 59–81.

Hodek, I. 1973. Biology of Coccinellidae. Junk, The Hague; Academia, Prague.

Huffaker, C. B., R. F. Luck, and P. S. Messenger. 1977. The ecological basis of biological control. *Proc. XV int. Congr. Ent.* (Washington, D.C.): 560–586.

Iperti, G. 1964. Les parasites des Coccinelles aphidiphages dans les Basses-Alpes et les Alpes-Maritimes. *Entomophaga* **9**: 153–180.

Pack, H. J. 1925. A biological study of certain ladybird beetles (Coccinellidae). Unpub. Ph.D. Thesis, Cornell University.

Putman, W. L. 1957. Laboratory studies on the food of some coccinellids (Coleoptera) found in Ontario peach orchards. *Can. Ent.* **89**: 572–579.

——— 1964. Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. *Can. Ent.* **96**: 1149–1155.

Richerson, J. V. and C. J. DeLoach. 1973. Seasonal abundance of *Perilitus coccinellae* and its coccinellid hosts and degree of parasitism in central Missouri. *Environ. Ent.* **2**: 138–141.

Shade, R. E., H. L. Hansen, and M. C. Wilson. 1970. A partial life table of the cereal leaf beetle, *Oulema melanopus*, in northern Indiana. *Ann. ent. Soc. Am.* **63**: 52–59.

Simpson, R. G. and C. C. Burkhardt. 1960. Biology and evaluation of certain predators of *Therioaphis maculata* (Buckton). *J. econ. Ent.* **53**: 89–94.

Sluss, R. 1968. Behavioural and anatomical responses of the convergent lady beetle to parasitism by *Perilitus coccinellae* (Shrank) (Hymenoptera: Braconidae). *J. invert. Path.* **10**: 9–27.

Smith, B. C. 1960. Note on parasitism of two coccinellids, *Coccinella trifasciata perplexa* Muls. and *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae) in Ontario. *Can. Ent.* **92**: 652.

——— 1961. Results of rearing some coccinellid (Coleoptera: Coccinellidae) larvae on various pollens. *Proc. ent. Soc. Ont.* **91**(1960): 270–271.

——— 1965*a*. Differences in *Anatis mali* Auct. and *Coleomegilla maculata lengi* Timb. to changes in the quality and quantity of the larval food. *Can. Ent.* **97**: 1159–1166.

——— 1965*b*. Growth and development of coccinellid larvae on dry foods (Coleoptera: Coccinellidae). *Can. Ent.* **97**: 760–768.

Smith, B. C. and R. R. Williams. 1976. Temperature relations of adult *Coleomegilla maculata lengi* and *C. m. medialis* (Coleoptera: Coccinellidae) and responses to ovipositional stimulants. *Can. Ent.* **108**: 925–930.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods, 6th ed. The Iowa State University Press, Ames.

Tauber, M. J. and C. A. Tauber. 1976. Environmental control of univoltinism and its evolution in an insect species. *Can. J. Zool.* **54**: 260–265.

van den Bosch, R. and P. S. Messenger. 1973. Biological control. Intext Series in Ecology, Intext Educ. Publ., New York.

Whitcomb, W. H. 1967. Field studies on predators of the second-instar bollworm, *Heliothis zea* (Boddie) (Lepidoptera: Noctuidae). *J. Ga ent. Soc.* **2**: 113–118.

Whitman, R. J. 1975. Natural control of the European corn borer, *Ostrinia nubilalis* (Hübner), in New York. Unpub. Ph.D. Thesis, Cornell University.

Wigglesworth, V. B. 1972. The principles of insect physiology, 7th ed. Chapman and Hall, London.

(Received 5 August 1977)