TEMPERATURE-DEPENDENT SURVIVAL AND HATCHING RATE OF EGGS OF SEVEN SPECIES OF COCCINELLIDAE

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Abstract

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The eggs of seven species of locally occurring coccinellids were reared at constant temperatures. The survival of eggs to hatching, rate, and thermal requirements for hatching were determined. The results were used to evaluate the importance of thermal adaptation of coccinellids in selecting them as biological control agents and in determining the relative species composition of locally occurring faunas of coccinellids.

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Résumé

Les oeufs de sept espèces locales de coccinellidés ont été gardés à des températures constantes. La survie des oeufs jusqu'à l'éclosion, le taux d'éclosion et les besoins thermiques jusqu'à l'éclosion ont été déterminés. Les résultats ont servi à évaluer l'importance de l'adaptation thermique des coccinellidés qui doivent servir d'agents de contrôle biologique et à déterminer la proportion relative des espèces au sein des faunes locales de coccinellidés.

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Introduction

Southwestern British Columbia has over 25 species of aphidophagous coccinellids (Belicek 1976) but only six are consistently encountered in crops (Frazer and Gilbert 1976). Despite the abundance of potential competitors, *Coccinella undecimpunctata* L. became abundant and widely distributed in southwestern British Columbia by 1970 (Frazer and Gilbert 1976), having been introduced in Washington in 1965 (Gordon 1985).

The impact of the establishment of *C. undecimpunctata* on resident populations of aphids and coccinellids is not known. Is there future risk of importing a species with high impact on Russian wheat aphid, for example (Naranjo et al. 1990), that could deleteriously affect resident predators that attack a broader range of local species of aphids? Polyphagous natural enemies, although primarily vertebrates, have accrued the largest number of detrimental effects on non-target species (Howarth 1991).

The responses of coccinellids to temperature may provide some evidence to aid in the evaluation of relative competitiveness and adaptability to local climates. Temperature requirements of aphids vary geographically for the same species and between species; the thermal requirements of their parasites and hyperparasites vary similarly but are always higher than their host in a given location (Campbell et al. 1974). The thermal requirements for development of 20 species of predators of aphids, of which six were coccinellids, were correlated with voltinism and microclimates associated with habitats (Honěk and Kocourek 1988).

This paper examines oviposition and survival of eggs and the rate of temperature-dependent development of eggs of seven species of aphidophagous coccinellids at three constant temperatures. The temperature relationships for development in the laboratory are used to predict development in the field. The relevance of the findings to biological control and to explain the relative abundance of locally occurring species is discussed.

Methods and Materials

Rearing. Adult *Coccinella californica* Mannerheim, *C. trifasciata* L., *C. undecimpunctata* L., *C. septempunctata* L., *Cycloneda polita* Casey, *Adalia bipunctata* (L.), and

Hippodamia convergens Guerin-Meneville were collected when encountered during the summer of 1989 in southwestern British Columbia. Over 100 adults were collected of each species except *C. septempunctata*; only one *C. septempunctata* was found, not enough to produce large enough numbers for all experiments. Adult females were placed individually in Petri dishes and supplied with an abundance of pea aphids, *Acyrthosiphon pisum* (Harris), and moistened filter paper. The Petri dishes were left overnight at 17.2 ± 0.05°C (mean ± SE). Eggs produced after 16 h were used to start and augment the rearing of each species.

Rearing was done in cages supplied by forced air, and provisioned with four 15-cm-diameter plastic pots containing 8–18 broad bean plants (*Vicia faba* L. cv. Broad Windsor) heavily infested with pea aphids (Forbes et al. 1985). Fresh pots of aphid-infested beans were added as required until at least 200 adult coccinellids were available from which the eggs for experiments were produced.

Experiments. The females used to produce eggs for experiments were 4–10 weeks old and were the progeny of the field-collected adults. Single female coccinellids were removed from stock rearing cages and placed in clear plastic milk cups (35 cm^3) with abundant pea aphids and moist filter paper. Females were picked at random from the stock cages each day but no female was used 2 days in a row. The cups were inspected for eggs every 1–3 h. Egg batches produced in a cup were counted, and the cup was given an identifying number and randomly assigned to one of three constant-temperature cabinets until at least 40 egg batches for each species were present in each cabinet. The time of oviposition was taken to be the time between inspections. Average hourly temperatures (± SE) in each cabinet were 12.0 ± 0.001, 16.0 ± 0.002, and 20.0 ± 0.002°C with 16L:8D photoperiod and an average illumination intensity of 86.5 ± 2.5 $\mu Em^{-2}s^{-1}$ in the cups.

The eggs in each cup were examined every 12 h until larvae emerged. Distilled water was added to cups as required to keep the air saturated with water. The time of hatch was calculated as the mid-point of the inspections. The number of eggs in each cup and the number of larvae produced were recorded. The time required to hatch, the rate (1/time in days), and the survival rate of larvae from each egg mass were calculated.

Statistics. Standard errors for the thermal thresholds (ρ) and the times required for eggs to hatch, DD^{ρ}, in day-degrees above each threshold, were estimated according to Campbell et al. (1974). All means are followed by their standard errors. Test statistics for hypothesis testing are represented as an F statistic followed by degrees of freedom and the level of significance. Duncan's new multiple range test was used to determine significance between means. GLM procedure (SAS®) was used to test for linearity, equality of slopes (β), and y-intercepts (α) of the rate (1/days to hatch) versus temperature relationship for each species of coccinellid.

The temperature at which no development occurs (ρ) is the x-intercept in terms of the regression of rate of development versus temperature and is estimated as the y-intercept divided by the slope of the line ($-\alpha/\beta$). SAS® GLM does not include a test for equality of x-intercepts, but a test was developed using the NLIN procedure. This was done by using a regression model that used common average values of α and β for all species to produce a residual mean square and then repeating the analysis with species-specific estimates of α and β, derived from simply linear regressions, to produce the mean square for the hypothesis.

Field Temperatures. An Omnidata Easylogger®, fitted with thermistor temperature sensors and programmed to record minimum and maximum temperatures each hour, was housed in a louvred box 1 m over sod in the centre of agricultural production in the Fraser Valley. The hourly data for spring and summer of 1987, 1988, and 1989 were electronically retrieved. The minimum and maximum temperatures each day were used to estimate the number of day-degrees (DD) above the estimated threshold temperature, ρ, of each species

Table 1. Numbers (±SE) of eggs per batch, percentage of eggs hatching, and mean days to hatch at various temperatures for seven species of coccinellids. There were 40 egg batches at each temperature and species combination. Means in the same column followed by the same letter are not significantly different (Duncan's new multiple range test at $p \leq 0.05$)

Species	Temperature, °C	Eggs per batch	% hatch	Days
C. septempunctata	16	20.3 (4.3)	34.9 (6.20)	7.7 (0.18)
	20	40.6 (9.1)	45.6 (5.54)	4.8 (0.21)
	avg.	33.0 a		
A. bipunctata	12	14.5 (1.00)	24.0 (3.39)	14.3 (0.21)
	16	19.0 (2.73)	30.8 (5.25)	6.3 (0.13)
	20	15.1 (1.09)	44.1 (3.81)	4.2 (0.06)
	avg.	14.2 b		
H. convergens	12	15.5 (1.04)	0.0 (—)	— (—)
	16	17.8 (1.49)	45.1 (4.19)	7.9 (0.08)
	20	12.2 (0.94)	61.2 (4.19)	4.9 (0.05)
	avg.	13.5 b		
C. californica	12	13.4 (1.83)	22.7 (4.30)	21.1 (0.39)
	16	12.4 (1.33)	56.8 (4.54)	8.0 (0.07)
	20	11.5 (1.15)	71.2 (4.50)	4.7 (0.04)
	avg.	11.9 b		
C. undecimpunctata	12	11.4 (1.56)	9.0 (2.86)	21.2 (0.34)
	16	12.8 (0.90)	63.8 (4.74)	7.5 (0.06)
	20	11.1 (0.87)	54.7 (5.46)	4.4 (0.10)
	avg.	11.3 b		
C. polita	12	8.9 (0.68)	41.3 (5.81)	17.2 (0.35)
	16	9.6 (0.62)	68.3 (4.83)	7.2 (0.06)
	20	11.4 (1.56)	54.3 (4.99)	4.6 (0.07)
	avg.	8.9 c		
C. trifasciata	12	9.3 (0.65)	27.9 (3.41)	20.8 (0.17)
	16	8.4 (0.48)	72.3 (3.86)	8.5 (0.23)
	20	8.8 (0.60)	65.0 (3.78)	5.0 (0.4)
	avg.	8.6 c		

of coccinellid, derived from the egg hatch data. An algorithm (Frazer and Gilbert 1976) that assumes sinusoidal fluctuations between minimum and maximum temperatures was used when minimum temperatures were below ρ.

The estimates of DD and ρ for each species were used to determine when eggs laid in the field on the 1st day of each month of the growing season would have hatched if subjected to the recorded field temperatures.

Results

The numbers of eggs of *C. septempunctata* and their source from the progeny of only one female were biased for statistical purposes but the data are included because of the interest in this species.

Fecundity. The average number of eggs laid per batch by each species (Table 1) varied significantly (31.27, 6/534, 0.0001) among species but not among temperatures (2.51, 2/534, 0.08) within a species. *Coccinella septempunctata* produced more than 4-fold as many eggs per batch as the least fecund *C. trifasciata* and *Cycloneda polita*. The other four species had intermediate mean numbers of eggs in their batches.

Rate and Threshold Temperature of Egg Hatch. Eggs hatched in 14–21 days at the lowest temperature, 12°C, and in 4–5 days at the highest temperature, 20°C, depending upon species. No eggs of *H. convergens* hatched at 12°C (Table 1). The relationship between the rate of hatching (1/days) and temperature contained no significant non-linearity for any species tested. The intercepts, α, (77.66, 5/600, <0.0001) and slopes, β,

Table 2. Regression parameters (± SE) for rate of development (1/days to hatch) as a linear function of temperature, the resulting thermal threshold of hatching, ρ, and time to hatch, DD^ρ, for seven species of coccinellids. Values in columns followed by the same letter are not significantly different (Duncan's new multiple range test at $p \leq 0.05$). Data for *C. septempunctata* were not included in analyses

Species	α	β	N	ρ	DD^ρ
A. bipunctata	−0.174 (0.009)	0.0208 (0.0005)	94	8.4a (0.30)	48.1a (1.2)
C. polita	−0.180 (0.007)	0.0200 (0.0004)	106	9.0b (0.21)	49.9a (1.0)
C. californica	−0.201 (0.005)	0.0207 (0.0003)	100	9.7c (0.16)	48.4a (0.7)
C. trifasciata	−0.194 (0.006)	0.0199 (0.0004)	136	9.7c (0.18)	50.2a (0.9)
H. convergens	−0.189 (0.012)	0.0199 (0.0007)	87	9.5c (0.33)	50.2a (1.6)
C. undecimpunctata	−0.244 (0.164)	0.0237 (0.0009)	91	10.2d (0.37)	42.1b (1.6)
C. septempunctata	−0.178 (0.054)	0.0193 (0.0029)	8	9.2 (1.42)	51.7 (7.8)
Weighted average group c and a			9.65	49.4	

(9741.25, 1/600, <0.0001) of the regressions of temperature versus hatching rate of each species were significantly different from each other (Table 2). That α and β differ is not sufficient proof that the threshold temperatures for egg hatch ($\rho = -\alpha/\beta$) would also differ. The analyses referred to above were used to test for equality of ρ's. In that analysis, the hypothesis that the threshold temperatures for each species were the same was rejected (10.89, 5/602, <0.0001).

Adalia bipunctata had the lowest threshold temperature (8.4°C) and *C. undecimpunctata* had the highest threshold (10.2°C) but the lowest DD. The other species had intermediate values for both statistics (Table 2).

Survival of Eggs. The survival rate of eggs in egg masses (Table 1) differed significantly among species (20.31, 6/619, 0.0001) and among temperatures (36.0, 2/619, 0.0001) with significant interaction (4.08, 10/619, 0.0001) between species and temperature (Table 1).

Survival rates were significantly lower at 12°C than at higher temperatures for all species except *C. septempunctata* which was not tested at 12°C. No eggs of *H. convergens* survived at 12°C. Maximum survival occurred at the intermediate temperature in all species except *A. bipunctata* and *C. californica* which survived better at 17°C. Subtracting the threshold temperature (Table 2) of each species from the temperatures in the chambers provided an estimate of ''effective temperature'' (Fig. 1) that each temperature provided each species.

Effect of Threshold Temperatures in the Field. The number of days required for an egg batch of each species to hatch, given oviposition on the first of a month, was estimated using the number of day-degrees above each species' threshold and time required for hatching, DD^ρ (Table 2). Eggs of *A. bipunctata* would always be the first to hatch. The additional time required for eggs of the other species to hatch varied from a half a day to as long as a week depending on the month and species. Eggs of *C. trifasciata* would always have been the last to hatch (Table 3).

Discussion

Climate and the Existing Fauna. The experimental temperatures used in this study were those normally experienced in the field by aphids in the Vancouver area. In the last 40 years, average daily maximum, minimum, and mean temperatures ranged from 9.4, 2.1, and 5.8°C, respectively, in March, to 21.9, 12.6, and 17.3°C in July. Maximum temperatures seldom exceed 30°C and when they do, the temperature accumulations per day for all species tested would not exceed those that would be experienced at a constant temperature of 20°C.

Overwintering adult coccinellids are usually first seen here in mid-April each year, almost 2 months after strawberry aphids have emerged from eggs on strawberry (Frazer

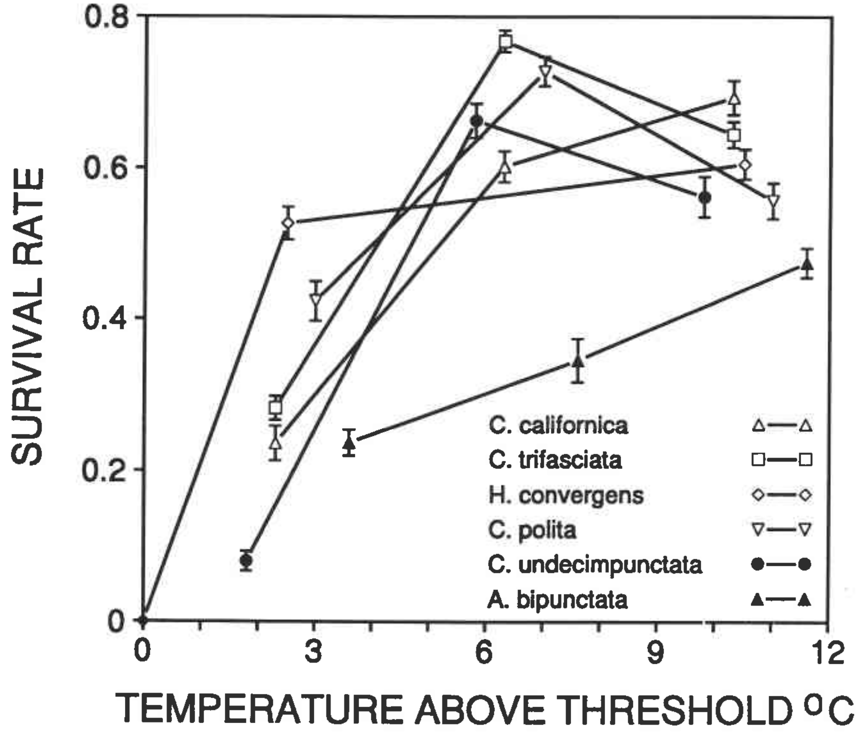

FIG. 1. Rates of survival of eggs of six species of Coccinellidae versus the effective temperatures (see text) above each species' threshold temperature.

Table 3. Number of days required for eggs of seven species of coccinellids to hatch if eggs were laid in the field on the 1st day of various months during 3 years

Date	*Coccinella californica, C. trifasciata, H. convergens*	*Cycloneda polita*	*Coccinella undecimpunctata*	*Adalia bipunctata*	*Coccinella septempunctata*
May 1987	9.5	7.5	8.5	6.5	24.0
June	10.0	9.0	9.0	7.5	11.0
July	9.5	8.5	9.0	7.5	11.5
August	7.0	6.5	6.0	6.0	7.0
April 1988	27.5	25.5	27.0	21.5	39.5
May	13.0	11.5	12.0	11.5	19.5
June	13.5	13.0	13.0	12.0	15.0
July	9.0	8.5	8.5	8.0	11.5
August	7.0	6.5	6.5	5.5	7.5
April 1989	22.5	19.5	22.0	18.0	28.5
May	13.0	9.5	10.5	8.0	15.0
June	6.0	5.0	5.0	5.0	5.5
July	9.0	8.0	8.0	7.5	9.5
August	7.0	6.5	6.5	6.0	7.5

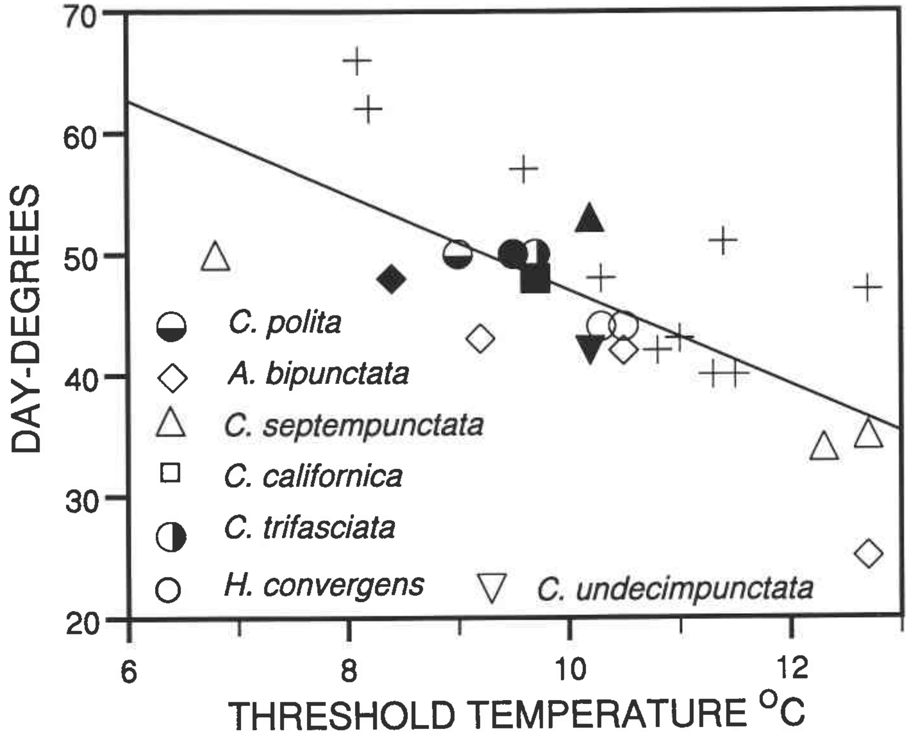

FIG. 2. Day-degrees required for egg hatch versus the threshold temperature for species of coccinellids from this study (filled symbols) and from the studies of (+ and hollow symbols) Honěk and Kocourek (1988), Obrycki and Tauber (1978, 1981, 1982, 1983), Olszak (1987), Okrouhlá et al. (1983), Baumgärtner et al. (1987), Brown (1972), Chakrabarti et al. (1988), Butler (1982), Butler and Dickerson (1972), and Orr and Obrycki (1990).

and Raworth 1985). Strawberry aphids here have a hatching threshold near 3°C (Frazer and Raworth 1984) and that of the pea aphid is 4°C (Frazer and Gilbert 1976). The delay in activity of coccinellids ensures aphids a period of almost unmolested reproduction.

The first species of coccinellid able to consume the aphids of early spring and oviposit would have an initial competitive advantage over later appearing species. First-instar larvae are poor searchers with limited chances of survival unless they emerge near prey (Frazer et al. 1981) which is more likely at high densities of aphids. The advantage of ovipositing early could be lost if later ovipositing species were able to hatch and develop faster (Takahashi 1989) because aphidophagous coccinellids are cannibalistic. Eggs and young larvae are readily eaten by adults and older larvae, and consumption of unhatched eggs provides an early and often essential meal to young larvae.

In spring, *A. bipunctata* eggs can hatch as much as 4 days before those of the other species tested here. That advantage is reduced to a day or less in summer when temperatures are well above the thresholds of all species (Table 3) but even a half day at the elevated temperatures of summer allows considerable time, on a day-degree scale, for predation. The developmental advantages of *A. bipunctata* over the other species tested are not manifested in abundance relative to the other species on crops or shade trees but it is the first species seen in spring (unpublished data). The significantly lower survival rate of eggs at all temperatures it would experience in this climate probably reduces the ability of *A. bipunctata* to capitalize on its more rapid rate of development. The high mortality may have been due to experimental temperatures being constant and combined with high humidity but, if so, the other species, with the exception of *H. convergens*, were not affected.

The long developmental time of *H. convergens* in the field (Table 3) combined with intolerance to low temperatures makes it a poor competitor in this climate. The species is rarely seen here and only in low numbers in mid-summer (unpublished data) but is a common and abundant coccinellid throughout most of North America (Gordon 1985).

The introduced *C. undecimpunctata* seems well adapted to this maritime climate as suggested by Dobzhansky (1931). It is able to hatch in the field before the indigenous *C. californica* and *C. trifasciata* and has maximal survival rates over the range of temperature likely to be experienced here. The thermal pre-adaptation likely accounts for its ability to rapidly become a dominant species in our fauna (Frazer and Gilbert 1976).

Cycloneda polita has survival rates and developmental rates similar to the indigenous *Coccinella* species (Tables 1, 3) but the lower fecundity seen in this study (Table 1), if it also occurs in the field, may account for its very limited numbers in the field (Ives 1981).

The three indigenous *Coccinella* species are the most abundant in crops and have maximal survival of eggs at the temperatures experienced in the field, which compensates for their less than maximal fecundities and rates of development.

Biological Control. The thermal requirements of eggs of coccinellids are poorly known but those for which data have been published present some interesting trends (Fig. 2). Threshold temperatures and thermal requirements are derived from the same regression and hence are not independent of each other or without error. Each point in Figure 2 could be shown with confidence ellipses if sufficient data were provided in all publications. The eggs of four locally occurring coccinellids tested here are rather tightly clumped on the graph indicating, as in aphids and their parasites, that predators of aphids are also highly adapted to their indigenous habitats. The thermal advantages of *A. bipunctata* over the other species and the reason the introduced *C. undecimpunctata* could successfully compete here are evident from their lower thresholds and requirements, respectively.

It is usually advisable to search for new potential parasites of univoltine pests in climates similar to the area where it is intended to release them. Climatic similarity is a requisite to ensure synchrony of the pest with the parasite. For predators of pests with many generations each year, like aphids, the strategy should be different. A species with earlier and faster development than *A. bipunctata* could be more effective at reducing the early aphid populations that now increase unchecked.

Coccinellids with lower threshold temperatures or thermal requirements than those found here do exist but none would hatch earlier than *A. bipunctata* in the field based on the same analysis as was done to prepare Table 3. To have a thermal advantage coccinellids would have to have both lower thresholds and requirements than those in Figure 2. However species or strains with those combined characteristics would likely be found in cooler or more northerly areas than have been investigated to date. This may be because researchers currently seek species from areas with similar rather than cooler climates.

Although important attributes of potential natural enemies are many, thermal adaptations are one of the easiest to measure and are essential to successful biological control.

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