

# Phenology of Three Coccinellid Species:<sup>1,2</sup> Thermal Requirements for Development<sup>3</sup>

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## ABSTRACT

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Three coccinellids, *Adalia bipunctata* L., *Coccinella transversoguttata* Brown, and *Coccinella septempunctata* L., show optimal preimaginal development and survival at temperatures between 26.7° and 29.4°C. Development of *A. bipunctata*, from oviposition to adult emergence, requires an accumulation of 263 heat degree days (*K*) above a theoretical threshold for development (*t*) of 9.0°C. *Coccinella transversoguttata* requires 218 heat degree days above 12.2°C. and *C. septempunctata*, an imported Palearctic species, requires an accumulated *K* value of 197 above 12.1°C. *Adalia bipunctata*'s low *t* value allows early-season development, when temperatures are low. In comparison *C. transversoguttata* and *C. septempunctata* can develop faster at higher summer temperatures because of their low *K* values. Based solely on thermal characteristics, the three coccinellid species may produce between 3 and 4 generations per year. However, the species differ in the degree to which they approach the maximum developmental rate in the field. These differences are determined by the species' differential prey specificity and diapause characteristics.

Recently, there has been considerable research on the phenology and developmental requirements of beneficial species (e.g. Campbell et al. 1974, Tauber and Tauber 1974, 1976, Neuenschwander 1975, Obrycki and Tauber 1978, Johnson et al. 1979). Such studies contribute to the efficiency of mass-rearing, and by providing a quantitative basis for predicting development and activity, they increase our ability to use beneficial species in pest management programs. Our present report is one in a series focused on the seasonal occurrence and activity of selected coccinellids in northeastern North America.

The three coccinellids we studied, *Adalia bipunctata* L., *Coccinella transversoguttata richardsoni* Brown, and *Coccinella septempunctata* L., are primarily aphidophagous. *Adalia bipunctata* occurs throughout the Holarctic, generally in arboreal habitats (Hodek 1973). It was reported as one of the two most common coccinellid species in southern Ontario peach orchards (Putman 1964). *Coccinella transversoguttata* occurs widely in North America (Brown 1962); in central Ontario it is one of the most abundant coccinellids in young red pine plantations (Gagné and Martin 1968) and in corn fields (Smith 1971). In contrast to these two species, *C. septempunctata* is distributed widely in the Palearctic and displays considerable phenological variability throughout its range (Hodek 1973). *Coccinella septempunctata* has been released several times in North America (e.g. Shands et al. 1970, 1972, Angalet et al. 1979, Cartwright et al. 1979, Tauber et al., unpublished) with variable success.

Because temperature is one of the most important factors in regulating seasonal development and activity of poikilotherms, we examined its influence on survival and development of each species. To describe the temperature-development relationship, we used two empirically derived values: *t* - the lower theoretical threshold for development, estimated by extrapolating the linear portion of the temperature-developmental velocity curve,

and *K* - the thermal constant, calculated from the equation  $K = y(d-t)$ , where *y* = mean developmental time (days), *d* = temperature (°C), *t* = theoretical threshold for development (°C).

In all tests, we used the 1st generation offspring of field-collected adults. *Adalia bipunctata* and *C. transversoguttata richardsoni* adults were collected in the Ithaca, NY area during the summer and fall and were maintained at L:D 16:8, 24° ± 1°C. Adult *C. septempunctata* were obtained from an established colony in NJ (see Angalet et al. 1979). Field-collected adults of all 3 species were provided with water, a wheat<sup>(R)</sup>-protein food mixture (Tauber and Tauber 1971), and a constant supply of both *Acyrtosiphon pisum* (Harris) (pea aphids), and *Myzus persicae* (Sulzer) (green peach aphids). The resulting egg clusters were distributed among constant temperature conditions with 3 replicates/temperature (see Table 1, 2, 3). On the day of hatching we transferred the 1st instar larvae to individual vials. *Adalia bipunctata* and *C. transversoguttata* were fed *A. pisum*; *C. septempunctata* were fed *A. pisum* and *M. persicae*. The larvae were checked daily for ecdysis.

Developmental times (in days) were established for each preimaginal life stage (ecdysis to ecdysis) and for total development. When recording development of 4th instars, we included the "prepupa", an immobile stage preceding the pupal ecdysis. Statistical analysis for each species followed that outlined by Obrycki and Tauber (1978). In all ANOVA tests for linearity we used a 0.05 level of significance.

The method we used to calculate *t* and *K* values is based upon the linear portion of the temperature-developmental velocity relationship for insects. This estimation of *t* and *K* assumes that very little development occurs in the lower curvilinear portion of the temperature-developmental rate relationship (see Campbell et al., 1974). Although considerable development may occur below (Mellors and Helgesen 1978) and above (Logan et al. 1976) the linear portion of the curve, linearly derived *t* and *K* values provide a good basis for accurately estimating development in the field for many species.

<sup>1</sup> Coleoptera: Coccinellidae.

<sup>2</sup> *Adalia bipunctata*, *Coccinella transversoguttata*, *Coccinella septempunctata*.

<sup>3</sup> Received for publication April 17, 1980.

Table 1.—Development and mortality of *Adalia bipunctata* under constant temperatures ( $\pm 1^\circ\text{C}$ ; L:D 16:8).

|                       | Developmental times (days; mean of replicate means $\pm$ S.E.) |               |               |               |               |               |
|-----------------------|--|---------------|---------------|---------------|---------------|---------------|
|                       | 15.6°  | 18.3°         | 21.1°         | 24°           | 26.7°         | 29.4°         |
| egg                   | 6.5 $\pm$ .5   | 4.7 $\pm$ 1.9 | 3.8 $\pm$ .1  | 3.1 $\pm$ .1  | 2.4 $\pm$ .1  | 2.1 $\pm$ .1  |
| 1st instar            | 5.6 $\pm$ .6   | 4.0 $\pm$ 2.1 | 2.5 $\pm$ .2  | 2.6 $\pm$ .2  | 2.2 $\pm$ .3  | 2.0 $\pm$ .1  |
| 2nd instar            | 3.5 $\pm$ .2   | 2.7 $\pm$ .2  | 2.0 $\pm$ .1  | 1.5 $\pm$ .1  | 1.3 $\pm$ .1  | 1.2 $\pm$ .2  |
| 3rd instar            | 4.2 $\pm$ .2   | 2.8 $\pm$ .2  | 2.1 $\pm$ .1  | 1.8 $\pm$ .2  | 1.3 $\pm$ .1  | 1.3 $\pm$ .02 |
| 4th and prepupa       | 9.2 $\pm$ .4   | 6.8 $\pm$ .3  | 4.9 $\pm$ .1  | 4.4 $\pm$ .5  | 3.6 $\pm$ .4  | 3.3 $\pm$ .2  |
| pupa                  | 10.6 $\pm$ .4  | 7.9 $\pm$ .1  | 5.9 $\pm$ .1  | 4.4 $\pm$ .02 | 3.7 $\pm$ .2  | 3.2 $\pm$ .1  |
| total develop.        | 39.6 $\pm$ .7  | 28.8 $\pm$ .3 | 21.3 $\pm$ .1 | 17.8 $\pm$ .5 | 14.5 $\pm$ .8 | 13.0 $\pm$ .4 |
| No. in each replicate | (25,23,20)   | (25,28,22)    | 25,27,25)     | (38,25,24)    | (26,29,28)    | (26,25,21)    |
|                       | % Mortality (mean of replicate percentages $\pm$ S.D.)         |               |               |               |               |               |
|                       | 21 $\pm$ 9   | 20 $\pm$ 2    | 18 $\pm$ 11   | 30 $\pm$ 9    | 11 $\pm$ 2    | 35 $\pm$ 10   |

Table 2.—Development and mortality of *Coccinella transversoguttata* under constant temperatures ( $\pm 1^\circ\text{C}$ ; L:D 16:8).

|                       | Developmental times (days; mean of replicate means $\pm$ S.E.) |                |                |                |                |
|-----------------------|--|----------------|----------------|----------------|----------------|
|                       | 18.3°  | 21.1°          | 23.3°          | 26.7°          | 29.4°          |
| egg                   | 5.2 $\pm$ 1.1  | 4.1 $\pm$ 0.1  | 3.6 $\pm$ 0.5  | 2.5 $\pm$ 0.5  | 2.5 $\pm$ 0.4  |
| 1st instar            | 4.8 $\pm$ 0.4  | 3.3 $\pm$ 0.1  | 2.7 $\pm$ 0.2  | 2.0 $\pm$ 0.2  | 1.6 $\pm$ 0.3  |
| 2nd instar            | 3.3 $\pm$ 0.4  | 2.3 $\pm$ 0.3  | 2.3 $\pm$ 0.3  | 1.5 $\pm$ 0.2  | 1.2 $\pm$ 0.1  |
| 3rd instar            | 3.8 $\pm$ 0.4  | 2.8 $\pm$ 0.3  | 2.4 $\pm$ 0.3  | 1.7 $\pm$ 0.2  | 1.2 $\pm$ 0.2  |
| 4th and prepupa       | 7.8 $\pm$ 1.0  | 6.2 $\pm$ 0.8  | 4.6 $\pm$ 0.4  | 3.7 $\pm$ 0.4  | 2.9 $\pm$ 0.3  |
| pupa                  | 8.3 $\pm$ 0.5  | 6.1 $\pm$ 0.3  | 5.1 $\pm$ 0.3  | 3.5 $\pm$ 0.2  | 3.0 $\pm$ 0.0  |
| total develop.        | 33.0 $\pm$ 1.6   | 24.9 $\pm$ 0.5 | 20.8 $\pm$ 1.5 | 14.9 $\pm$ 1.2 | 12.5 $\pm$ 0.5 |
| No. in each replicate | (21,24,20)   | (15,21,27)     | (32,23,35)     | (20,27,27)     | (22,28,26)     |
|                       | % Mortality (mean of replicate percentages $\pm$ S.D.)         |                |                |                |                |
|                       | 22 $\pm$ 3   | 32 $\pm$ 14    | 21 $\pm$ 12    | 12 $\pm$ 18    | 15 $\pm$ 21    |

Table 3.—Development and mortality of *Coccinella septempunctata* under constant temperatures ( $\pm 1^\circ\text{C}$ ; L:D 16:8).

|                       | Developmental times (days; mean of replicate means $\pm$ S.E.) |                |                |                |                |                |
|-----------------------|--|----------------|----------------|----------------|----------------|----------------|
|                       | 18.3°  | 21.1°          | 24°            | 26.7°          | 29.4°          | 32.2°          |
| egg                   | 4.3 $\pm$ 0.1  | 3.5 $\pm$ 0.2  | 3.3 $\pm$ 0.0  | 2.2 $\pm$ 0.1  | 2.2 $\pm$ 0.0  | 2.0 $\pm$ 0.1  |
| 1st instar            | 4.2 $\pm$ 0.2  | 3.3 $\pm$ 0.2  | 2.1 $\pm$ 0.1  | 2.0 $\pm$ 0.2  | 1.3 $\pm$ 0.1  | 1.2 $\pm$ 0.1  |
| 2nd instar            | 3.1 $\pm$ 0.1  | 2.1 $\pm$ 0.2  | 1.7 $\pm$ 0.1  | 1.2 $\pm$ 0.1  | 1.1 $\pm$ 0.1  | 1.0 $\pm$ 0.1  |
| 3rd instar            | 3.3 $\pm$ 0.1  | 2.5 $\pm$ 0.0  | 1.9 $\pm$ 0.1  | 1.7 $\pm$ 0.1  | 1.2 $\pm$ 0.2  | 1.2 $\pm$ 0.1  |
| 4th and prepupa       | 7.8 $\pm$ 0.1  | 5.1 $\pm$ 0.1  | 3.9 $\pm$ 0.2  | 3.0 $\pm$ 0.2  | 2.6 $\pm$ 0.1  | 2.5 $\pm$ 0.1  |
| pupa                  | 8.1 $\pm$ 0.1  | 5.5 $\pm$ 0.1  | 4.5 $\pm$ 0.1  | 3.5 $\pm$ 0.3  | 2.9 $\pm$ 0.0  | 2.5 $\pm$ 0.1  |
| total develop.        | 30.7 $\pm$ 0.4   | 21.7 $\pm$ 0.1 | 17.0 $\pm$ 0.2 | 13.6 $\pm$ 0.2 | 11.2 $\pm$ 0.1 | 10.4 $\pm$ 0.1 |
| No. in each replicate | (22,22,21)   | (31,31,31)     | (30,30,27)     | (31,30,30)     | (30,30,27)     | (30,26,26)     |
|                       | % Mortality (mean of replicate percentages $\pm$ S.D.)         |                |                |                |                |                |
|                       | 19 $\pm$ 6   | 3 $\pm$ 3      | 5 $\pm$ 5      | 14 $\pm$ 10    | 12 $\pm$ 15    | 22 $\pm$ 8     |

cies (e.g. Tauber and Tauber 1976, Wright and Laing 1978, Johnson et al. 1979).

For the species we studied, the ecologically meaningful temperatures — the temperatures encountered by the beetles at our latitude — generally fall within the linear portion of the curve.

### Results

*Adalia bipunctata*.—Our data (Table 1) indicate that between 15.6° and 29.4°C the rate of development for each life stage (except the 1st and 3rd instars) and for the total life cycle was linearly related to temperature (Fig. 1). Excluding the 21.1°C data, the developmental

rate of 1st instars was also linear within this range of temperatures. The developmental rate of 3rd instars was linearly related to temperature between 15.6° and 26.7°C (Table 1).

Theoretical thresholds ( $t$ ) for development of all *A. bipunctata* life stages fell between 7.8° and 10.9°C (Table 4). Total development required 263 heat degree days ( $K$ ) above 9°C. Mortality was highest at 29.4°C and lowest at 26.7°C.

*Coccinella transversoguttata*.—For most life stages and for total development the relationship between developmental rates and temperature was linear (Fig. 1). The rate of egg development was linear from 18.3° to

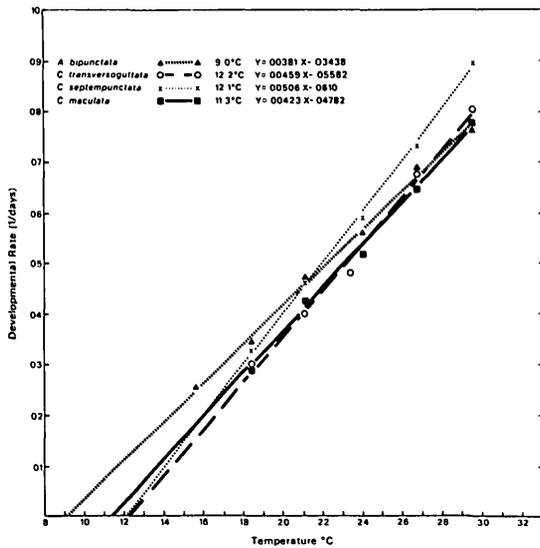


FIG. 1.—Developmental velocities for *Adalia bipunctata*, *Coccinella transversoguttata*, *Coccinella septempunctata*, and *Coleomegilla maculata* (from oviposition to adult emergence). Intercepts on temperature axis are the lower theoretical thresholds for development (*t*). Data for *C. maculata* are from Obrycki and Tauber (1978).

26.7°C, and the pupal developmental rate was linear when results from 23.3°C were excluded.

The *t* values for *C. transversoguttata* fell between 10.8° and 13.7°C (Table 4); total development required 218 heat degree days above 12.2°C. Mortality varied between replicates but generally was lower at higher temperatures (Table 2).

*Coccinella septempunctata*.—The rate of pupal development was linear over the entire range of temperatures. The 2nd instar, 3rd instar, 4th ‘‘prepupal’’ stage, and the total life cycle showed linear developmental rates at temperatures from 18.3° to 29.4°C (Fig. 1); the developmental rates for the egg and 1st instar were linear for all temperatures excluding 26.7°C. At 32.2°C the rate of total development leveled off and was only slightly faster than development at 29.4°C.

Theoretical thresholds for development ranged from 6.8° to 13.4°C; total development required 197 heat degree days above 12.1°C (Table 4). The egg stage had a very low *t* value and required approximately 50 heat degree days before hatching. Mortality was highest at 18.3°C and 32.2°C.

Discussion

*A. bipunctata*.—Although the rate of development for *A. bipunctata* was more rapid at 29.4°C, we consider 26.7°C to be the optimum temperature because the mean mortality was approximately 25% lower at 26.7°C. It appears that the thermal requirements for *A. bipunctata* larvae from New York and Ontario are similar; for an Ontario population the mean developmental time at 20°C (Putman 1964) fell between the values that we recorded at 18.3° and 21.1°C. However, it should be noted that we reared larvae on the aphid *A. pisum*, and that Putman (1964) reared larvae on the aphid *Rhopalosiphum rufomaculatum* Wilson.

Four previous studies examined aspects of the temperature-development relationships of Palearctic populations of *A. bipunctata*. Three of these studies considered only the larval or larval-pupal development at relatively few constant temperatures. Larvae from populations in England (Blackman 1965) and Finland (Hämäläinen 1976) showed developmental rates similar to larvae from the Ithaca population. However, development times for *A. bipunctata* larvae from central Germany (Jöhnssen 1930) were longer than those in the Ithaca population.

Finally, based upon Ellingsen’s (1969) values for a population from Finland, we calculated that the thermal requirements for pupal development were *t* = 7.6°C, *K* = 99.8 heat degree days and for total development were *t* = 8.5°C, *K* = 244.8 heat degree days. Thus, the Finnish population had lower thresholds for both pupal and total development, and its development was more rapid at any given temperature than development of *A. bipunctata* from Ithaca. Ellingsen (1969) also reared *A. bipunctata* under temperatures that fluctuated from 8° to 28°C ( $\bar{X}$  = 18°C) and observed no difference between developmental rates at a constant 18°C and at the fluctuating temperatures.

*C. transversoguttata*.—The optimum temperature for *C. transversoguttata* was 29.4°C. Mortality rates at 26.7° and 29.4°C were similar; however, total development was 2.4 days faster at 29.4°C.

At 21°C, *C. transversoguttata* from central Ontario had a mean total developmental time (oviposition to adult emergence) of 39.6 days (Gagné and Martin 1968), which is much longer than the 24.9 days that we observed at 21.1°C. In both studies, the egg and pupal developmental times were similar but the larval development took twice as long in the Ontario population.

Table 4.—Developmental thresholds (*t*) and thermal constants (*K*) for *Adalia bipunctata*, *Coccinella transversoguttata*, and *Coccinella septempunctata* ( $\bar{X}$ ±S.E.)

|                            | <i>A. bipunctata</i> |           | <i>C. transversoguttata</i> |            | <i>C. septempunctata</i> |           |
|----------------------------|----------------------|-----------|-----------------------------|------------|--------------------------|-----------|
|                            | <i>t</i> (°C)        | <i>K</i>  | <i>t</i> (°C)               | <i>K</i>   | <i>t</i> (°C)            | <i>K</i>  |
| egg                        | 9.2±1.2              | 43.2±2.2  | 10.8±2.5                    | 41.6±6.4   | 6.8±0.6                  | 50.4±1.1  |
| 1st instar                 | 7.8±0.7              | 42.3±1.0  | 13.1±1.1                    | 26.7±1.5   | 13.4±1.7                 | 21.9±1.5  |
| 2nd instar                 | 9.4±1.2              | 22.8±1.2  | 12.1±2.6                    | 21.9±2.9   | 12.5±1.7                 | 18.2±1.6  |
| 3rd instar                 | 10.9±2.3             | 21.1±2.6  | 13.7±2.5                    | 20.4±2.7   | 11.9±2.0                 | 22.7±2.3  |
| 4th instar and ‘‘prepupa’’ | 7.8±1.2              | 69.8±3.3  | 12.4±1.5                    | 50.3±4.0   | 12.9±0.5                 | 42.1±1.1  |
| pupa                       | 10.2±1.0             | 61.4±2.3  | 12.4±0.9                    | 50.9±2.5   | 12.1±0.7                 | 50.7±1.4  |
| total develop.             | 9.0±0.9              | 262.8±9.0 | 12.2±1.3                    | 218.2±14.5 | 12.1±0.4                 | 196.8±4.4 |

This disparity may result from differences in (a) food or (b) photoperiod or (c) larval thermal requirements in the two experiments. Gagné and Martin (1968) used woolly pine needle aphids, *Schizolachmus piniradiatae* Davidson and L:D 12:12.

*C. septempunctata*.—A temperature of 29.4°C gave both rapid development and relatively low mortality for *C. septempunctata*. In comparison with central European populations, the *C. septempunctata* population from the Ithaca, NY area has a similar  $t$  value but a lower  $K$  value. For example, based upon data summarized by Hodek (1973), we calculated a  $t$  value of 11.9°C and a  $K$  value of 216 heat degree days for total development of a *C. septempunctata* population from Czechoslovakia (c.f. 12.1°C and 196.8 heat degree days for the Ithaca population). From data for a central German population (Jöhnsen 1930), we calculated a  $t$  of 11.9°C and a  $K$  of 269 heat degree days for total development. These and other studies from England (Blackman 1965), Finland (Hämäläinen 1976), India (Sethi and Atwal 1964), Israel (Bodenheimer 1943), and Norway (Sundby 1966) indicate, as discussed by Hodek (1973), that the thermal requirements for development of *C. septempunctata* are relatively stable over its broad latitudinal Palearctic distribution. The North American population appears to share this stable characteristic.

#### Seasonal Activity

Early in the season, when temperatures are near the developmental thresholds, *A. bipunctata*, with its low  $t$  value (Fig. 1), could begin development earlier than *C. transversoguttata* or *C. septempunctata*. It also would begin development earlier than *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae), which we previously showed has a  $t$  value of 11.3°C and a  $K$  value of 236 heat degree days (Obrycki and Tauber 1978). However, at higher temperatures, *A. bipunctata*'s large  $K$  value results in a longer developmental time than that required by the other 3 species. Thus, late in the season, when temperatures are high and consistently above threshold values, *C. septempunctata*, which has the lowest  $K$  value, would complete development in the shortest period of time (Fig. 1).

To predict the maximum number of generations per year in our area for the above 4 coccinellid species, we estimated heat accumulations based on daily maximum and minimum temperatures<sup>4</sup> (Baskerville and Emin 1969). We summed heat accumulations for the period between the initiation of vernal activity and an estimated time of diapause induction (Aug. 31). In these calculations we have rounded down the maximum number of generations (Table 5) to account for the preoviposition period and assumed that our laboratory derived  $t$  and  $K$  values are directly applicable to field conditions. These 2 assumptions will be tested during later field studies.

Based solely on the thermal requirements for development, we predict that the native species, *A. bipunctata*, would produce between 3 and 4 generations, while the maximum for the other 2 native species, *C. maculata*

and *C. transversoguttata*, is approximately 3 generations (Table 5). In comparison, field studies in the Ithaca, New York area (Pack, 1925) indicate that *A. bipunctata* and *C. maculata* produce 2 to 3 generations, while *C. transversoguttata* produces only 2 generations each year. Thus, of the three native species, *C. maculata* comes closest to realizing the maximum number of generations per year, whereas *A. bipunctata* and *C. transversoguttata* fall short of their annual potential by almost an entire generation.

Putman (1964) reported that low aphid densities reduce the annual number of generations of several coccinellid species in Ontario. The effect he observed appeared to be greater on the aphidophagous species, *A. bipunctata* and *C. transversoguttata*, than on the polyphagous *C. maculata*. We propose that while the maximum developmental rate is set for each of the three species by temperature, i.e. the accumulation of heat-degree days ( $K$ ) above  $t$  characteristic of an area, food can have a major role in determining the actual rate of development. The degree to which food affects the rate of development is strongly influenced by the species' characteristic degree of prey specificity; food is more limiting to the aphidophagous species than to the polyphagous *C. maculata*.

In some species of coccinellids, food may affect voltinism by influencing aestival diapause (Hagen 1962, McMullen 1967). This is not the case for the 3 native species we studied, none of which enter aestival diapause in Ithaca (Pack 1925, Obrycki and Tauber unpublished). However, it is possible that food availability may reduce the developmental potential of the three species by influencing the timing of the induction of autumnal diapause.

The seasonal life cycle of the introduced species, *C. septempunctata* presents a different problem from the species discussed above. Based on its thermal requirements and prevailing temperatures, this species is capable of producing 3 generations per year (Table 5). However, in our study area it is univoltine and throughout its Palearctic distribution it is uni- or bivoltine (Hagen 1962, Hodek 1973). The number of generations per year is reduced by a prolonged aestival-autumnal-hibernal diapause.

Finally, in considering attributes that underlie the utility of biological control agents in temporary agroecosystems (Ehler 1977, Ehler and Miller 1978), we conclude that of the four coccinellid species we have studied, the polyphagous *C. maculata* would be the most amenable for manipulation and use. First, unlike *C. septempunctata*, its diapause does not restrict it to a single generation per year and thus it can prey on pest populations over a longer time period. Second, of the three native multivoltine species, its development is the most reliably predicted on the basis of heat accumulations because it is the least affected by prey scarcity. Third, its polyphagous feeding habits may make manipulation with artificial food sprays possible (see Hagen et al. 1971). Such attributes (see Ehler 1977, Ehler and Miller 1978) make *C. maculata* particularly adaptable to temporary agroecosystems.

<sup>4</sup> Monthly Meteorological Summary, Division of Atmospheric Sciences, Cornell University.

Table 5.—The estimated number of generations each year for *A. bipunctata*, *C. maculata*, *C. transversoguttata*, and *C. septempunctata* based upon laboratory-derived *t* and *K* values and daily max/min field temperatures calculated from the date of vernal activity to August 31.

| Species                     | Initiation of vernal activity | Heat accumulations <sup>a</sup> above ( <i>t</i> values) | Generations      |                    |
|-----------------------------|-------------------------------|--|------------------|--------------------|
|                             |                               |  | Predicted        | Observed           |
| <i>A. bipunctata</i>        | May 10 <sup>b</sup>           | 1028 (9.0°C)   | 3.7              | 2–3 <sup>b</sup>   |
| <i>C. maculata</i>          | May 15 <sup>b,c</sup>         | 773 (11.3°C) <sup>c</sup>                                | 3.1 <sup>c</sup> | 2–3 <sup>b,c</sup> |
| <i>C. transversoguttata</i> | May 20 <sup>b</sup>           | 657 (12.2°C)   | 2.8              | 2 <sup>b</sup>     |
| <i>C. septempunctata</i>    | May 20                        | 657 (12.1°C)   | 3.1              | 1                  |

<sup>a</sup> Calculations of heat accumulations followed Basekerville and Emin (1969) using temperature data for 1979 from the Monthly Meteorological Summary, Division of Atmospheric Sciences, Cornell University.

<sup>b</sup> from Pack (1925).

<sup>c</sup> from Obyrcki and Tauber (1978, 1979).

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