Effect of Constant and Varying Temperature on Development, Feeding, and Survival of *Adalia bipunctata* L. (Col., Coccinellidae)

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The effect of constant and varying temperatures on development, feeding and survival of *Adalia bipunctata* L. was tested. For a varying temperature range of 8-28°C, an incubator was used in which the temperature followed a diurnal cycle with fixed means, maximums, and minimums. Development of the species is possible within most of the range. There was no difference in development of eggs and pupae, and probably not of larvae. Aphid consumption was 10.6 per cent higher at varying temperature, but the difference was not significant. The higher vitality at varying temperature was significant; the survival period of starved larvae increased by 16.7 to 37.8 per cent.

Odum (1959, pp. 105-106) proposed that the stimulating effect of varying temperature, in the temperate zone at least, should be accepted as a well-defined ecological principle, and that special emphasis should be laid on it, since there has been a tendency to conduct experimental work in the laboratory under constant temperature conditions.

The effect of constant and varying temperatures on the rate of development of insects has been extensively investigated, but records of the effect on feeding and survival are few.

Most of these studies may be grouped into classes, according to the method used to vary the temperature: (i) a fraction of the developmental period is spent continuously at one temperature and the remainder at a different constant temperature; (ii) exposure of the insects to two abrupt changes of temperature daily; (iii) a series of artificially constructed patterns in which the temperature varies smoothly and regularly in a theoretical diurnal cycle with fixed means, maximums and minimums; (iv) the most natural approach, by which templates are made from thermographs of natural habitats and used to control incubation temperatures.

An important question is how to summarize the pattern of variable temperature to evaluate its effect on the insect. The mean is an adequate representation of pattern only as long as the temperature remains within the zone in which the rate of development is linearly related to temperature. Therefore, the choice of ranges and the mean temperature is important.

In the present study, experiments were carried out in an incubator that gave smooth consistent cyclical temperature fluctuations.
The pattern was selected to agree as closely as possible with temperatures prevailing in the field at the time of occurrence of the insects. Experiments were also carried out at 7 constant temperatures to study the relationship between development and temperature.

MATERIAL AND METHODS
Material for these experiments was collected at Vollebekk, Ås, southern Norway. Normal mean air temperature at Ås is 14.4°C in June, 16.8°C in July, and 15.6°C in August (Meteorologic data for Ås 1967). According to microclimatic measurements in the vegetation (Sundby, unpublished) a range of 8-28°C with mean 18°C was chosen in an incubator, where the temperature followed a diurnal cycle with fixed means, maximums, and minimums (the mechanism is discussed by Sundby, unpublished). The incubator had 16 hours of light per day. Experiments at constant temperatures were carried out under the following conditions:

Temperature (°C) 6 9 12 15 18 21 28
Hours of light per day 0 0 0 24 18 0 16
It was not possible to arrange identical light periods at all temperatures. Thermohygrometers showed a range of 50-80 per cent relative humidity.

To avoid individual variations, one pair of A. bipunctata was used as the origin of stock culture, except for data on incubation of eggs and survival of larvae, where effect of constant and varying temperature was tested.

The Aphid species used as prey was Myzus persicae (Sulzer).

RESULTS
Results of experiments at constant and varying temperature are summarized in Table I, and displayed in more detail as histograms in Fig. 1.

The development of larvae seems to be more susceptible to varying temperature than eggs and pupae. Total larval development was sig-
Table I. Effects of constant and varying temperatures on development, aphid consumption and survival of starved larvae in *A. bipunctata*

<table>
<thead>
<tr>
<th></th>
<th>Constant 18°C</th>
<th>Varying 8–28°C</th>
<th>t-test of the difference</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>X ± S. E.</td>
<td>N</td>
</tr>
<tr>
<td>(a) Duration of development (in days)</td>
<td></td>
<td></td>
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<tr>
<td>Eggs</td>
<td>1808</td>
<td>5.24 ± 0.01</td>
<td>1038</td>
</tr>
<tr>
<td>Larvae</td>
<td>54</td>
<td>13.4 ± 0.1</td>
<td>46</td>
</tr>
<tr>
<td>Pupae</td>
<td>40</td>
<td>10.0 ± 0.1</td>
<td>32</td>
</tr>
<tr>
<td>(b) Number of aphids eaten per larvae</td>
<td>40</td>
<td>188 ± 13.7</td>
<td>32</td>
</tr>
<tr>
<td>(c) Survival (in days) of newly emerged larvae offered water only</td>
<td>53</td>
<td>2.9 ± 0.1</td>
<td>46</td>
</tr>
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Significantly (4.5 per cent) retarded. Fig. 1 reveals in detail, however, that some larval instars were accelerated and some retarded.

Voracity of larvae was increased 10.6 per cent at varying temperature, but it was not statistically significant. Vitality proved to be higher at varying temperature than at constant. Survival of starved larvae was prolonged 16.7 to 37.8 per cent (Fig. 1), and this was statistically significant. Mortality during larval and pupal stages was 28.6 per cent at constant temperature and 22.2 per cent at varying temperature. The highest value of hatched eggs from one female was found at varying temperature.

Experiments on duration of development at 7 different temperatures were performed as an aid towards discussing the difference between constant and varying temperature experiments. Numbers of individuals (N) that completed development at the different temperatures were as follows:

°C 6 9 12 15 18 21 28
N 0 0 0 21 40 12 29

The relationship between temperature and duration of developmental stages is shown in Fig. 2. Standard errors were never greater than 0.3 days, and were most frequently 0.1 days.

Larvae kept at 6°C were completely inactive and consumed no aphids; at 9°, four (of 36 newly emerged larvae) reached 2nd instar, and one came to 4th instar; at 12°, four (of 31) reached the prepupal stage, but died; at 21°, mortality in larval and pupal stages was 52.0 per cent. All these four series had total darkness.

DISCUSSION

Records of the effect of alternating temperatures from older literature may seem confusing, especially if we do not take into consideration how the temperature range is related to the temperature-development curve. Odum (1959) concludes that it is not certain whether variation in itself is responsible for the accelerating effect, or whether high temperature causes more growth than is balanced by low temperature. Howe (1967) states that there is little evidence in the literature that temperature fluctuations influence the rate of development of eggs. But if varying temperature is represented by a mean, at the lower temperatures the eggs will hatch sooner than expected, in the medial range they will hatch when expected, and at high temperatures the hatching may be delayed.
The results of the present study showed no difference in rate of development at constant and varying temperatures, but perhaps a little retardation of larval development at varying temperature.

As seen from Fig. 2, the range 8-28°C is quite suitable for development, but 8° might be too low. The exact threshold for development and optimal temperature cannot be read from the curve.

In addition to temperature change, Hodek (1958) reported that the rate of development and mortality of Coccinella septempunctata was affected by the length of the light period. He found 12 per cent retarded development in total darkness, whereas with 24 or 12 hours of light there was little retardation. In Fig. 2 of the present study a correction of values measured in total darkness would have reduced the irregularity at 21°C and given smoother curves.

Duration of development of A. bipunctata was reported by Jönnsen (1930) from Cologne. In Fig. 2, his values are $x_1 = 13-16$ days larval development at 22-23°C, and $x_2 = 12$ days at 25°C. These values lie above mine, which may indicate that A. bipunctata has been adapted to develop at lower temperatures in our latitude.

As to the effect of varying temperature on feeding, the present experiments may indicate that feeding follows the same pattern as duration of development. Parker (1930) reports that dry weight of food consumed by grasshoppers at alternating temperatures amounts to a 24 per cent reduction from the amount used during the nymphal stage at constant temperature (reduction in length of nymphal stage was 30 per cent). Another possibility is that feeding (like vitality) is stimulated by varying temperature. Sundby (unpublished) found that pupae of Coccinella septempuncta-
were heavier at varying temperatures (same incubator as used for *A. bipunctata*).

The report of Gawande (1966), who fed aphids to *Chilomenes sexmaculata* F.B., is confusing, since feeding rate was stimulated when larvae were kept at low temperature for 8-16 hours, whereas temperature had negative effect on larvae kept for only one hour. For adults the situation was reversed.

For *A. bipunctata*, the larger survival of larvae and lower mortality seem to be the most convincing 'stimulatory effect of variable temperature'. To the author's knowledge this has not previously been described.

REFERENCES


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