The effect of temperature on the activity of Carabidae (Coleoptera) in a fallow field

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Abstract. In 1992–1994, the activity of ground surface arthropods was investigated on a fallow field divided into small plots with different regimes of weed management. Daily operated pitfall traps were placed in a transect across the field. The aim of the study was to investigate the effect of temperature on the magnitude of total arthropod catches. The pooled catches of all arthropod species were poorly correlated with temperature since its effects were damped by differences in timing of peak abundance of the species. To compensate for the effect of this variation groups of species with similar patterns of annual variation of abundance were selected. The regressions of pooled catch on average daily temperature were then calculated for periods of their peak occurrence when changes of their abundance and/or behaviour were minimum. Seven abundant carabid species were selected and regressions calculated for periods of April 20–May 13 (Bembidion lampros, Harpalus tarsus, Pseudocillus cupreus), June 25–July 25 (H. tarsus, P. cupreus), and August 8–September 9 (Amara convexicrura, H. affinis, H. distinguentus, Pseudoophonus rufipes). By this procedure a significant effect of temperature on carabid activity was shown, similar for different species groups and periods. The catch size increased in the average by 6.3 percentage points per 1°C increase of average temperature. Using this temperature/catch size relationship daily catches of several species were recalculated on a standard temperature of 20°C. This procedure decreased the variation of daily catches by 5–31%. The decrease was proportional to the variation of daily temperatures during the period of sampling.

INTRODUCTION

Pitfall trapping is a widely used method of investigating the activity of ground surface arthropods. It provides better results in comparison with other methods, e.g., direct counting or D-Vac sampling (Adis, 1979; Volkmar et al., 1994). Arthropod activity is influenced by several factors including temperature. Differences in activity associated with variation in density of plant cover and probably caused by differences in microclimate have been demonstrated frequently (Novák, 1967; Petruška, 1971; Skuhrová et al., 1971; Baker & Dunning, 1975; Ericson, 1979; Wallin, 1985; Honěk, 1988; Honč & Martinková, 1991). In contrast, temperature effects due to changing weather are difficult to detect. Sometimes it has been concluded that the contribution of weather to the changes of overall arthropod activity on ground surface is small (e.g., Volkmar et al., 1994). The absence of demonstrable temperature effects is because variation due to temperature may be shown only after a period of time, at least 2–3 weeks. Meanwhile changes also occur in the abundances of different species, due to demographic processes in arthropod populations. The occurrence of population peaks of different species is not synchronous. A temporal succession of population peaks of dominant species with different abundance may compensate for temperature effects.
Honěk & Martinková (1993) showed that temperature effects may be demonstrated by using data from species with similar seasonal dynamics. This paper presents a calculation of temperature effects using daily catches of seven abundant carabid species over 3 years. It aims to demonstrate a general relationship between carabid activity and temperature rather than investigating species specific differences. It also attempts to estimate the decrease of variation in catch size following its recalculation for selected species based on the amount which would be captured under a standard temperature. This procedure tested the applicability of the general relationship to particular species.

MATERIAL AND METHODS

Arthropod sampling

The research was performed in a 25 × 25 m experimental fallow field established at Praha-Ružyně. The field was bordered by crop stands (spring mustard in 1992, and oats in 1993 and 1994), a hedge and a road. Each year the field was ploughed in November and harrowed and rolled in March. No crop was sown and the field became overgrown with weeds established from the natural seed bank and roots of perennials. No pesticides were applied. The field was divided into five 5 × 5 m plots. The five plots were: left intact and weedy (control), mowed early (June 22, 1992; June 8, 1993; June 8, 1994), and mowed late (July 29, 1992; July 19, 1993; July 22, 1994), or mowed and superficially cultivated at either early or late term of mowing. The ground inhabiting arthropods were collected by pitfall traps. The traps were plastic cups (7 cm diam., 8 cm deep) dug into the soil, with the rim at the soil surface. The traps were screened from rain and sunshine by a dish wrapped in aluminium foil. No bait was used. A few pieces of soil at the bottom of the cups provided shelter for trapped arthropods. The traps were operated from the moment of establishing early ploughed plots until late August and were emptied daily, at 8:00 a.m. The captured arthropods were determined, counted and released. On weekends and during periods of the author’s absence the traps were not operated. A transect line of 6 traps was placed at the interface of experimental plots, and their catches were pooled when investigating daily variation of abundance. The traps were operated in 1992–1994, from mid-April until mid-October.

Calculating temperature effects on catch size

The procedure used for calculating temperature effects requires some preliminary considerations. The variation in catch size is influenced by several factors including activity (a product of abundance and intrinsic urge for foraging) and temperature. One may suppose that the effect of both factors may be separated by calculating running means of the catches (which parallel trends in activity) and the differences between running means and actual catches (net effects of temperature). The regression of the differences on temperature is then calculated. However, this procedure does not provide acceptable results since daily to-day changes of temperature are not random, but the weather usually changes over periods of at least several days. This long-period variation also affects the running means of the catches and decreases the magnitude of residuals due to temperature. During long periods of warm weather, positive departures from (high) catches are small, while a period of cold weather decreases the magnitude of negative departures. Preliminary calculations revealed that this kind of bias obscures the temperature/catch size relationship. Therefore a procedure based on a logical assumption that (if the seasonal variation of abundance has a sinus-wave form) the changes of abundance during a short period around the population peak are small, without a monotonic trend for increase or decrease was adopted. Several species with parallel peaks of activity were selected and the regression of catch size on temperature was calculated. The procedure had following steps: (1) selecting several species with similar seasonal variation of abundance, (2) pooling their daily catches at the period of 20–30 days around their common population peak, (3) transforming the daily catches to percentages of the maximum catch for a given year and (4) calculating the regression of transformed data (summed over the years of observation) on average daily temperature (T). Pooling data of several species appeared helpful. Besides temperature, activity of each species is influenced by prey availability, humidity and other factors, whose effects probably differ between species. This species specific sensitivity to to various environmental factors obscure the temperature/catch size relationship, and pooling decreases the effects of these “noise” factors. It also increases the numbers of individuals
Fig. 1. Seasonal variation of daily catches (expressed as the proportion of the maximum catch in a given year) of carabid species used for calculating relationship between catch size and temperature. The periods of peak abundances used for calculation of the catch/temperature relationship are indicated by hatched lines and heavy bars below the abscissas. Each day of trapping in 1992–1994 period is indicated by a separate column. A – *Harpalus tardus*; B – *Ptecticus cupreus*; C – *H. affinis*; D – *H. distinguendus*; E – *Amara convexiuscula*; F – *P. rufipes*. The data for *Rembidion lampros* are not shown due to low representation of this species in catches throughout most of the season.
considered for calculating the regressions and decreases the effects of their random variation. Transforming the data to percentage points did not change their distribution and, consequently, there was no need for transformation of the data (e.g., to arcsin values). For the calculation data from years when temperatures in the selected period were similar, i.e., the annual mean of average temperatures for the days of pitfall sampling did not differ by > 4°C were used. Using data from years with more different average temperatures would increase the scatter along the abscissa but not along the ordinate (due to percentage point transformation). This asymmetry would decrease the slope of regression line and invalidate the results. Meteorological data were obtained from the Prague Airport, about 3 km from the site of the study.

RESULTS

The effect of temperature on catch size

The daily servicing of the traps enabled the catch size to be related to the average temperature over 24 h periods of catching. No relationship was found between the pooled total catch of all arthropods and temperature. The correlation between catch size and temperature calculated for 2-month periods, spring (April–May), early summer (June–July), or late summer (August–September) were not statistically significant. Although the catch size decreased at temperatures below 10°C, above this threshold the variation was enormous and obscured any temperature effect.

For the calculation of temperature effects, 7 abundant carabid species were selected: *Amara convexiuscula* (Marsham), *Bembidion lampros* (Herbst), *Harpalus affinis* (Schrank), *H. distinguendus* (Duftschmid), *H. tardus* (Panzer), *Poecilus cupreus* (L.) and *Pseudoophonus rufipes* (DeGeer). Their population peaks occurred in the spring, early summer or late summer (Fig. 1).

In spring, the regression of pooled catches of *B. lampros*, *H. affinis*, *H. distinguendus*, *H. tardus* and *P. cupreus* on temperature was calculated for the period of April 20–May 13. Data from 1992 (average temperature at the days of capture were 10.5 ± 3.3°C) and 1994 (average temperature 11.1 ± 2.0°C) were used, whilst data from 1993 (average temperature 15.3 ± 3.5°C) were omitted. The regression (catch = 7.2 T – 29.9) predicted a 7.2 percentage points increase of catch size per 1°C increase of average temperature (Fig. 2). The results were highly significant (r² = 0.555, df = 18, P < 0.001).

In early summer, the regression of pooled catches of *H. tardus* and *P. cupreus* on temperature was calculated for the period of June 25–July 25. Data from 1992 (average temperature 19.1 ± 2.9°C) and 1994 (average temperature 21.6 ± 2.6°C) were used whilst data from 1993 (average temperature 14.2 ± 2.2°C) were omitted. The regression (catch = 6.3 T – 85.4) predicted a 6.3 percentage points increase of catch size per
Fig. 3. Pooled catches of *H. turdis* and *P. cupreus* in the early summer period (June 25 – July 25) in 1992 and 1994 plotted against average daily temperatures.

1°C of temperature increase (Fig. 3). The results were highly significant ($r^2 = 0.357$, df = 23, $P < 0.001$).

In late summer, the regression of pooled catches of *A. convexuscula, H. affinis, H. distinguendus* and *P. rufipes* on temperature was calculated for the period of August 8 to September 9. Data of all years, 1992 (average temperature 17.4 ± 4.3°C), 1993 (average temperature 14.3 ± 3.1°C) and 1994 (average temperature 16.4 ± 1.8°C), were used. The regression (catch = 5.3 T – 33.1) predicted a 5.3 percentage points increase of catch size per 1°C temperature increase (Fig. 4). The results were also highly significant ($r^2 = 0.486$, df = 45, $P < 0.001$).

The average increase of catch size per 1°C of temperature increase was 6.3 percentage points.

Recalculating catch size on a standard temperature

The generalised regression of catch size on temperature enables recalculating the daily catches on a quantity which would be captured if the temperature were constant. This procedure should eliminate variation due to temperature. Using data of the period when species abundance varies little the recalculation should reduce significantly variation of the results. Catches expected at 20°C using data for 3 carabid species, *Anchomenus dorsalis* (Fontoppidan), *Pseudoophonus griseus* (Panzet) and *P. rufipes* were calculated. The average catch of the period of recalculation was set as 50 percent abundance. Recalculating the data decreased the variation of daily catches by 5–31 percentage points (Table 1). The extent of decrease of variation differed between species and periods of the season. The periods investigated differed in the average temperature and in the extent of temperature variation. The decrease of catch size variation following the recalculation was
proportionate to the range of temperature variation over the period for which the recalculation was made (Fig. 5).

**Table 1.** Recalculating daily catches of species at a standard temperature of T = 20°C. Period of catching and number of days (N) for which the means were calculated (with non-zero catch of the species), mean catch (± SD) and its coefficient of variation [cv = (SD/mean) × 100], and mean recalculated catch (± SD) and its coefficient of variation (cv).

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>N</th>
<th>Mean catch ± SD</th>
<th>cv (%)</th>
<th>Mean recalculated catch ± SD</th>
<th>cv (%)</th>
</tr>
</thead>
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<tr>
<td>Anchomenus dorsalis</td>
<td>June 10–July 16, 1992</td>
<td>18</td>
<td>4.8 ± 3.3</td>
<td>69.3</td>
<td>5.9 ± 3.6</td>
<td>61.1</td>
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<tr>
<td></td>
<td>May 24–June 22, 1993</td>
<td>16</td>
<td>2.4 ± 1.2</td>
<td>50.4</td>
<td>3.3 ± 1.5</td>
<td>45.7</td>
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<tr>
<td></td>
<td>May 25–June 23, 1994</td>
<td>14</td>
<td>3.5 ± 2.1</td>
<td>60.4</td>
<td>6.0 ± 2.6</td>
<td>43.5</td>
</tr>
<tr>
<td>Pseudoephusa griseus</td>
<td>August 4–Sept. 4, 1993</td>
<td>14</td>
<td>2.5 ± 1.5</td>
<td>60.8</td>
<td>4.0 ± 1.9</td>
<td>46.5</td>
</tr>
<tr>
<td></td>
<td>August 1–Sept. 1, 1994</td>
<td>11</td>
<td>3.2 ± 2.6</td>
<td>82.4</td>
<td>3.3 ± 2.1</td>
<td>64.1</td>
</tr>
<tr>
<td>Pseudoephusa rufipes</td>
<td>April 22–May 6, 1993</td>
<td>7</td>
<td>2.4 ± 1.7</td>
<td>69.1</td>
<td>4.0 ± 1.6</td>
<td>38.3</td>
</tr>
<tr>
<td></td>
<td>April 21–May 19, 1994</td>
<td>8</td>
<td>2.8 ± 1.3</td>
<td>47.3</td>
<td>5.4 ± 1.9</td>
<td>35.6</td>
</tr>
</tbody>
</table>

**DISCUSSION**

The results enabled the effects of temperature on size of arthropod catches in pitfall traps to be quantified. The average increase calculated in this study by regression of daily catches on mean daily temperatures (6.3 percentage points per 1°C) was similar to 5.2 percentage points established in an earlier study (Honěk & Martinková, 1993) using decade averages of catches and temperatures. Although weather effects are less important for the determination of catch size than seasonal changes of abundance (Volkmar et al., 1994) their contribution could be significant. The fact that a significant temperature/catch size relationship was established is an argument in favour of the method used. An intentional selection of data convenient for analysis provided better results than a mechanically applied statistical procedure.

The mechanism of temperature effect on catch size is apparently behavioural. A rise in temperature increases the foraging activity but other factors contribute significantly. This may be concluded from a large proportion of residual variation in catch size persisting after recalculation on a standard temperature. Moisture of the soil surface modifies the activity substantially. Under similar temperatures, activity was greater on a wet surface after rainfall than during periods of drought. However, quantifying the availability of water for

![Fig. 5.](image-url) The relationship between the decrease of variation in catch size due to recalculation of catches on a standard temperature of 20°C [calculated as (cv catch – cv recalculated catch)/cv catch] and temperature variation (cv of average temperatures) in the period of catching.
surface arthropods was unsuccessful. Many factors including dew and access to deeper soil layers by soil cracks, intervene in estimating the effects of humidity on arthropod activity.

Several species included in this study are efficient predators (Skuhravý, 1959). As predation increases with predator surface activity temperature should be an important factor of predation intensity. Low temperatures are associated with a reduction of predation rates (cf. Ekblom et al., 1992). Average temperature in different years could vary by several degrees. Thus, in the course of this study, there was a 7°C difference between days of catching in the early summer periods of 1993 and 1994. This would cause a 40 percentage points difference in surface activity perhaps paralleled by a similar difference in predation activity. However, the effect of temperature is modified by thermoregulatory behaviour. Effects of low temperature may be compensated for by basking in the sunshine (Honěk, 1988). This is an important factor which modifies the surface activity in cold and humid years.

Recalculating the size of pitfall catches on a standard temperature may improve observations of seasonal dynamics of species abundance. In particular, this may compensate for an apparent variation of abundance in the spring and the autumn periods which is, in fact, due to seasonal variation of temperature (Honěk & Martinková, 1993). Using data recalculated on a standard temperature may reveal the hidden patterns of population changes in these periods which, usually, are compensated by temperature effects. Recalculation may enable temperature effects to be separated from physiological changes or behavioural patterns (e.g., effects of incipient or terminating hibernation), or population changes.

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REFERENCES


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