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# Temperature threshold for growth and temperature-dependent weight gain of field-collected *Tipula montana* (Diptera: Tipulidae)

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***Tipula montana*, Diptera, temperature, growth rate, development, instar, life-cycle**

**Abstract.** *Tipula montana*, an upland tipulid of northern Britain and generally considered a montane species, was collected from the northern heath habitat of Waskerley Common, County Durham. The growth rate of larvae of *Tipula montana* was monitored at temperatures ranging from 1°C to 15°C at long photoperiod of 18 h light and 6 h dark. There was no significant growth at 5°C. At 7°C and above, the growth rate increased significantly in larvae initially in instars II and III. However, the growth rate of larvae initially in instar IV was unaffected by temperature, probably due to nearing the onset of pupation. 7°C is the minimum mean monthly temperature found during the main growing season (May–September) at Waskerley Common. Temperature had no significant effect on the weight at which moults to subsequent instars occurred but did accelerate the larval development.

At Waskerley Common *T. montana* follows either a one- or two-year life-cycle. If adequate temperatures (i.e. > 7°C) are not maintained during the growing season, fluctuations could occur in the numbers of individuals following the two life-cycles, resulting in varying numbers of adults produced at each emergence.

## INTRODUCTION

*Tipula montana* Curtis (Diptera: Tipulidae) has been considered a montane insect, found in habitats with sparse vegetation and feeding on mosses and plant debris. Coe et al. (1950) stated that this species was found only above 700 m a.s.l. in the British Isles where all larvae are thought to have a two-year life-cycle (Galbraith et al., 1993). However, in May 1990, larvae of *T. montana* were found at Waskerley Common, County Durham (Todd, 1993), which has an altitudinal range between 350 m and 450 m a.s.l. A small number of adults had also been collected at this site between 1976 and 1978 (Coulson & Butterfield, 1980). Waskerley Common is a northern heath where heather (*Calluna vulgaris*) is managed for red grouse (*Lagopus lagopus scoticus*) and the larvae of *T. montana* feed mainly on living and dead *Campylopus introflexus*, (a moss introduced into Britain in 1941 from the Southern Hemisphere [Watson, 1968]). This moss colonises bare peat where *Calluna* has been recently burnt. Larvae of *T. montana* live below the soil surface to a depth of 2 cm.

The main function of the larval stage of a holometabolous insect is to store sufficient energy to complete their pupal and adult stages and thereby reproduce, which is particularly important in *T. montana* since the adult stage does not feed in this species. The rate of energy storage is governed primarily by temperature. Temperature, as well as nutrition, has been shown to significantly affect the rate and magnitude of larval growth and development in insects (e.g. Anderson & Cummins, 1979; Scriber & Slansky, 1981; Stamp & Bowers, 1990). Nolte & Hoffman (1992) found that in the dipteran *Diamesa incallida*, the number of generations produced per year was entirely dependent upon the water temperature. At Waskerley, *T. montana* follows either a one- or two-year life-cycle. In the one-year life-cycle, eggs hatch in August and September, larvae overwinter in instar II, pupate from late June and adults emerge in late July and August (Todd, 1993). The two-year life-cycle occurs if larvae following the one-year life-cycle fail to reach the required weight for pupation in June or July, resulting in them overwintering in instar IV and pupating, due to a photoperiodic response, in the following May and emerging in early June (Todd, 1993).

It is considered advantageous for insect larvae to complete development as fast as possible, and preference for a specific temperature, either by selection of an appropriate habitat or by changing position within a habitat, has been related to increased growth rate. To follow the shorter one-year life-cycle it is important for the larvae of *T. montana* to reach the appropriate weight in instar IV to allow pupation to occur in June/July.

This study examines the larval growth rates of *T. montana* when cultured at a range of constant temperatures in the laboratory, and also when transferred from lower to higher temperatures. Development time data for larvae collected at constant temperatures in the laboratory can provide estimates of development times in the field under fluctuating temperatures (Hagstrum & Milliken, 1991). Experiment I was carried out initially on larval instars II, III and IV, and Experiment II on instar II larvae. The study also considers how growth at these temperatures can be related to the temperatures found throughout the year in the natural habitat of *T. montana*.

## MATERIAL AND METHODS

Larvae of *Tipula montana* were collected by hand searching at Waskerley Common, County Durham (54°N, 2°W) in March and November 1992, and in May 1993. The ideal habitat for these larvae at Waskerley were areas which had been burnt within the previous ten years, with sparsely distributed short stands of heather, bare peat and at least 50% cover of the moss *Campylopus introflexus*, upon which the larvae feed. Such areas were searched thoroughly, removing the surface layer of peat to a depth of ca. 2 cm. The larvae were placed in a cool-box which was maintained at ca. 5°C and transported to Cambridge for laboratory studies. Samples of *C. introflexus* were also collected from the field site.

The number of larval instars was ascertained by measurement of the spiracular disc diameter (Coulson, 1956). There are four larval instars in *T. montana*. Each larva was weighed live using a Sartorius micro balance accurate to ± 0.001 mg, and placed in a 9 cm petri-dish containing moist Whatman filter paper and an adequate supply of live *C. introflexus*. Monthly mean live weights of the larvae at each temperature were determined and the spiracular disc diameter used to determine the instar of each larva (identified for *T. montana* by Todd [1993]).

In Experiment I, the cultures of *T. montana* larvae initially in instars II, III and IV were maintained at 1, 5, 10 and 15°C (accurate to ± 0.5°C). In Experiment II, cultures of larvae in instar II (used so that any change in growth rate in response to temperature could be monitored over a longer time) were maintained at the above four temperatures and also at 7°C (± 0.5°C), which was used as an additional intermediate temperature between 5°C, where no increase in growth occurred and 10°C, where a significant increase in growth occurred. Larvae reared at 1°C and 5°C initially were transferred to 7°C. A maximum of ten larvae from each larval instar were placed at each experimental temperature. In this way, the weight change and the growth of individual larvae through the instars could be monitored at a range of temperatures. Experiment I ran from March to July 1992 and Experiment II from November 1992 to October 1993.

## RESULTS

### EXPERIMENT I

#### Effect of temperature on weight

Fig. 1 shows the mean monthly weights of *Tipula montana* larvae, which were originally in the instar stated. In instar IV larvae (Fig. 1a) there was no significant difference

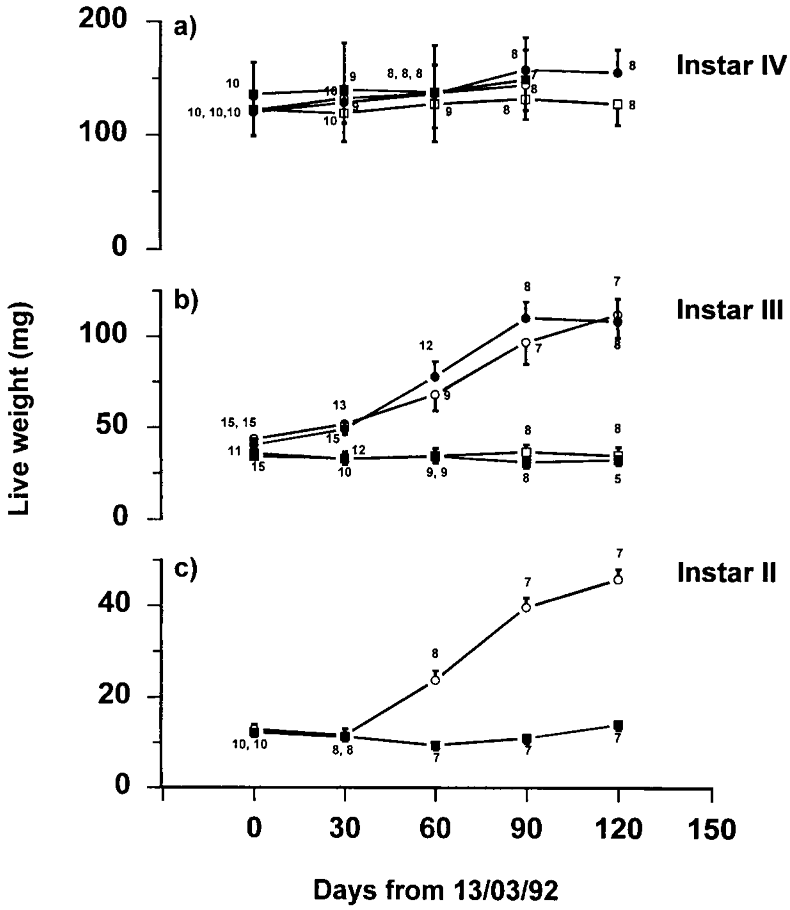


Fig. 1. Mean (± S.E.) monthly live weights (in mg) of *Tipula montana* larvae, initially in instar IV (a), instar III (b) and instar II (c), at a range of temperatures: □ 1°C, ■ 5°C, ○ 10°C, ● 15°C. The number of larvae is given for each data point.

between the initial mean weights of the larvae at any of the experimental temperatures. Similarly, at the end of the experiment, larval weights at each of the four temperatures were not significantly different. Additionally, there was no significant difference in the monthly growth rates of instar IV larvae (Table 1) at any temperature, even between 1 and 15°C ($t$ = 1.5, $df$ = 14, $p > 0.05$). Therefore, temperature did not have a significant effect on growth rate under the experimental conditions.

Fig. 1b shows the mean monthly weights at four temperatures for larvae initially in instar III. There was no significant growth increase at either 1°C or 5°C within the experimental period. At both 1 and 5°C, there was no significant difference between the initial and final weights of the larvae, $t$ = 0.1, $df$ = 21, $p > 0.05$ and $t$ = 0.9, $df$ = 14, $p > 0.05$, respectively. There was also no significant difference between the initial mean weights at the two temperatures, $t$ = 0.3, $df$ = 24, $p > 0.05$, nor between the final mean weights, $t$ =

0.4, $df = 11$, $p > 0.05$. However, at both 10 and 15°C there was significant growth between the initial and final weights, $t = 5.0$, $df = 20$, $p < 0.001$ and $t = 5.2$, $df = 21$, $p < 0.001$, for 10 and 15°C respectively (Fig. 1b).

TABLE 1. Mean (in mg ± S.E.) monthly growth rates of *Tipula montana* larvae, initially in the instar stated, cultured at a range of temperatures (Experiment I) and surviving until the end of the experimental period. The number of larvae used is given in parentheses. NS indicates $p > 0.05$; * indicates $p < 0.05$ and ** indicates $p < 0.01$.

| Temperature (°C) | Instar | | | | | |
|---|---|---|---|---|---|---|
| | II | | III | | IV | |
| | | *t* | | *t* | | *t* |
| 1 | – | | 0.1 ± 0.9 (8) | | 1.5 ± 0.6 (8) | |
| | | – | | 0.6 NS | | 0.8 NS |
| 5 | 0.4 ± 0.8 (7) | | –0.9 ± 1.3 (5) | | 4.6 ± 3.8 (7) | |
| | | 2.5 * | | 4.0 ** | | 0.7 NS |
| 10 | 8.2 ± 3.0 (7) | | 17.1 ± 4.3 (7) | | 7.7 ± 2.7 (8) | |
| | | | | 0.01 NS | | 0.2 NS |
| 15 | – | – | 17.0 ± 8.1 (8) | | 9.0 ± 4.9 (8) | |

From Table 1, the monthly growth rate of instar III larvae at 1°C (0.1 ± 0.9 mg) was not significantly different to that at 5°C, nor was the monthly increase at 10°C significantly different to that at 15°C. Therefore, data from 1 and 5°C were pooled, as were data from 10 and 15°C. This showed that the mean monthly increase in live weight of the larvae was significantly greater at the higher temperatures, at 17.0 ± 4.3 mg, than at the lower temperatures, at 0.4 ± 0.8 mg, ($t = 3.8$, $df = 14$, $p < 0.01$), i.e. these larvae have a faster growth rate at higher temperatures.

Fig. 1c shows the mean monthly weights for larvae originally in instar II. No significant growth occurred at 5°C in these larvae between the initial and final weights ($t = 1.2$, $df = 15$, $p > 0.05$). At 10°C, however, significant growth did occur between the initial and final weights, $t = 13.3$, $df = 15$, $p < 0.001$. From Table 1, the monthly growth rate was significantly higher at 10°C than at 5°C.

Since the results from Experiment I indicated that there was no significant growth at 1 or 5°C in both instars II and III, but significant growth did occur at 10 and 15°C in these instars, it was considered important to determine if significant growth occurred in tipulid larvae at temperatures between 5 and 10°C. So, 7°C was chosen as an intermediate temperature.

Effect of temperature on development

Table 2 shows the final mean weight of larvae before the moult to the next instar stage (there were no data for 1°C as no moults occurred at this temperature). There was no significant difference in the mean final weight at either 5°C or 10°C for larvae moulting from instar II into instar III. For larvae moulting from instar III to instar IV at both 10°C and 15°C, again there was no significant difference in the mean final weights. Similarly, there was no significant difference in the mean final weights of fourth instar larvae which pupated at 10°C and at 15°C. Therefore, temperature did not have a significant effect on these final weights. No larvae moulted from instar III to instar IV, nor pupated at 5°C.

TABLE 2. Mean live weight (in mg ± S.E.) of *Tipula montana* larvae immediately prior to moulting into the subsequent instar, the number of larvae in parentheses and – indicating that no moult occurred. NS indicates $p > 0.05$.

| Temperature (°C) | Instar | | | | | |
|---|---|---|---|---|---|---|
| | II | | III | | IV | |
| | | *t* | | *t* | | *t* |
| 5 | 13.8 ± 1.3 (6) | | – | | – | |
| | | 1.2 NS | | | | |
| 10 | 16.7 ± 2.0 (5) | | 55.1 ± 4.1 (6) | | 118.0 ± 10.2 (3) | |
| | | | | 2.0 NS | | 0.8 NS |
| 15 | – | | 45.5 ± 2.5 (11) | | 130.9 ± 11.2 (5) | |

EXPERIMENT II

Effect of temperature on weights and growth rates of instar ii larvae

There was no significant difference in the initial mean weight of instar II larvae at each of the experimental temperatures (Table 3). The weight at the end of the experiment of each group of larvae (excluding those at 1 and 5°C) at each temperature were significantly greater than those of groups of larvae cultured at lower temperatures. At both 1 and 5°C, no significant increase in growth was observed during the experimental period (Day 0 to Day 90) in larvae of *T. montana* in instar II (Fig. 2, Table 3). The mean weights of the two groups of larvae at Day 0, and subsequently at Day 90, at 1 and 5°C, and the monthly growth were not significantly different. Additionally, the weights at the start and end of the experimental period of the larvae grown at 1°C, and at 5°C, were not significantly different. Therefore, no significant growth was apparent at these two temperatures.

When the animals growing at 1 and 5°C were transferred to 7°C, on Day 90, there was a rapid change with significant growth occurring by Day 150 (Fig. 2). Larvae originally grown at 1°C had a mean weight of 12.3 ± 0.8 mg on Day 90 which increased to 20.1 ± 2.1 mg by Day 150 ($t = 3.4$, $df = 16$, $p < 0.01$). Larvae originally grown at 5°C had a mean weight of 14.9 ± 1.4 mg on Day 90 and 31.9 ± 5.5 mg by Day 150 ($t = 2.4$, $df = 16$, $p < 0.05$).

There were no significant differences in mean weights of individuals when initially transferred to 7°C on Day 90 from 1 or 5°C ($t = 1.6$, $df = 16$, $p > 0.05$), but from Day 270 onwards the difference was significant, (37.4 ± 5.2 mg and 49.6 ± 2.0 mg respectively, $t = 2.2$, $df = 14$, $p < 0.05$), Fig. 2. Therefore, either the rate of growth was faster in those individuals originally at 5°C, than at 1°C (Table 3) or there was a longer delay in starting rapid growth at 7°C in those individuals transferred from 1°C.

In the monthly growth rates (Table 3), significant differences occurred between the groups of larvae growing at 5 and 7°C (ex 1°C). Additionally, significant differences

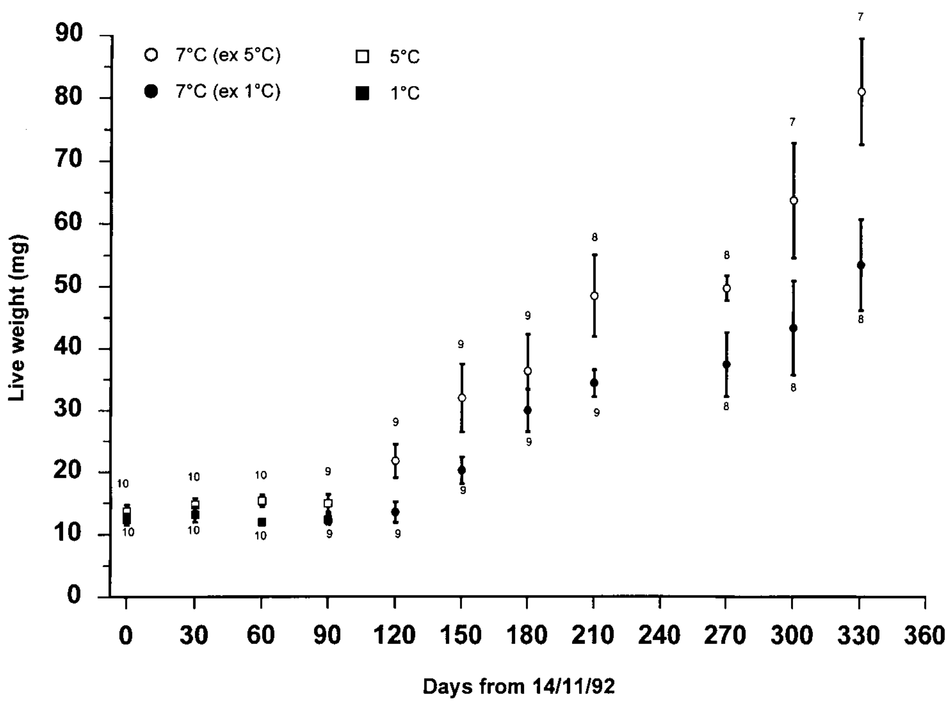


Fig. 2. Mean (± S.E.) monthly live weights (in mg) of *Tipula montana* larvae initially in instar II, and cultured initially at 1°C or 5°C and subsequently at 7°C. ■ 1°C, □ 5°C, ○ 7°C (ex 5°C), ● 7°C (ex 1°C). The number of larvae is given for each data point.

existed between the monthly growth rate of larvae cultured at 1°C and the two groups of larvae cultured at 7°C (ex 1°C) and 7°C (ex 5°C), ($t = 9.7$, $df = 8$, $p < 0.001$ and $t = 3.9$, $df = 8$, $p < 0.01$) respectively, and also between those larvae cultured at 5 and 7°C (ex 5°C), ($t = 3.3$, $df = 9$, $p < 0.01$).

As in instar II in Experiment I, significant growth occurred in these larvae through the year at both 10 and 15°C. In larvae grown at 10°C (Fig. 3a), significant growth increments occurred in the larvae after Day 30, the growth increase from Day 30 to 60 being due to moulting into instar III. The mean monthly weight of larvae on Day 60 was significantly greater than that on Day 30 ($t = 3.6$, $df = 18$, $p < 0.01$). After Day 210 (when larvae had moulted to instar IV), temperature no longer had a significant effect on the mean monthly weights. In those larvae cultured at 15°C (Fig. 3b), again significant growth occurred from Day 30 (the mean monthly weights were significantly different between Day 30 and 60, $t = 6.6$, $df = 16$, $p < 0.001$). As with the larvae at 10°C, after Day 210 temperature did not have a significant effect on the mean monthly weights.

The monthly growth rate during the experimental period for those larvae grown at 15°C was greater (but not significantly so) that for those grown at 10°C (Table 3). Larvae at 15°C had a significantly higher mean monthly growth rate than those larvae grown at 7°C (ex 1°C) and 7°C (ex 5°C); $t = 3.2$, $df = 17$, $p < 0.01$ and $t = 2.6$, $df = 17$, $p < 0.01$, respectively.

TABLE 3. Mean weight (in mg ± S.E.) of larvae of *Tipula montana* at the start and end of Experiment II which were initially in instar II, and the mean monthly growth rate (mg) for those larvae surviving until the end of the experimental period, n being number of larvae, n1 being the number of months, NS $p > 0.05$ * $p < 0.05$ *** $p < 0.001$.

| | Temperature (°C) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 5 | | 7 ex 1°C | | 7 ex 5°C | | 10 | | 15 |
| Initial weight | 12.4 ± 0.9 | | 13.7 ± 1.0 | | 12.3 ± 0.8 | | 14.9 ± 1.4 | | 12.6 ± 0.6 | | 13.4 ± 1.0 |
| n | 10 | | 10 | | 9 | | 9 | | 10 | | 10 |
| *t* | | 0.9 NS | | 1.1 NS | | 1.6 NS | | 1.5 NS | | 0.7 NS | |
| Final weight | 12.3 ± 0.8 | | 17.9 ± 1.4 | | 53.4 ± 7.3 | | 81.2 ± 8.5 | | 109.3 ± 10.3 | | 166.5 ± 11.8 |
| n | 9 | | 9 | | 8 | | 7 | | 5 | | 7 |
| *t* | | 1.6 NS | | 5.2 *** | | 2.4 * | | 3.6 *** | | 7.5 *** | |
| Mean monthly growth rate | −0.03 ± 0.6 | | 1.1 ± 0.8 | | 5.7 ± 1.4 | | 9.0 ± 2.3 | | 11.5 ± 3.3 | | 26.3 ± 6.4 |
| n1 | 3 | | 3 | | 8 | | 8 | | 11 | | 11 |
| *t* | | 1.1 NS | | 2.7 * | | 1.2 NS | | 0.6 NS | | 2.1 NS | |

## DISCUSSION

It is evident from this study that the minimum temperature at which significant growth can occur in larvae of *Tipula montana* is between 5 and 7°C. At temperatures below this, larvae were either unable to develop or development was severely limited. Experiment I had shown a clear difference between the growth rate at 5°C and that at 10°C in both instar II and III larvae. This had begged the question as to the effect on growth of larvae at an intermediate temperature.

As there was no significant growth at either 1 or 5°C in Experiment I or II, larvae at these temperatures were used as controls to demonstrate the repeatability of the results. This being the case, changes in growth rates of larvae could be monitored from the time of transfer from either 1 or 5°C to 7°C. This transfer had an appreciable effect on their development rate.

Temperature affects the rate and magnitude of larval growth in the cranefly, *Tipula abdominalis* (Vannote & Sweeney, 1985), as well as significantly affecting the rates of larval metabolism and development. The growth of *T. abdominalis* was positively correlated with temperature; larvae attained maximum size in the two warmest thermal regimes, whereas growth was severely restricted at lower temperatures. Morin & Dumont (1994) found that in lotic dipterans growth rates increased with an increase in temperature with a mean $Q_{10}$ of 1.78. The duration of development in insects decreases as the temperature increases and conversely, the rate of development increases in an approximately linear manner with increasing temperature, except at the extreme ends of the range for development (Chapman, 1979).

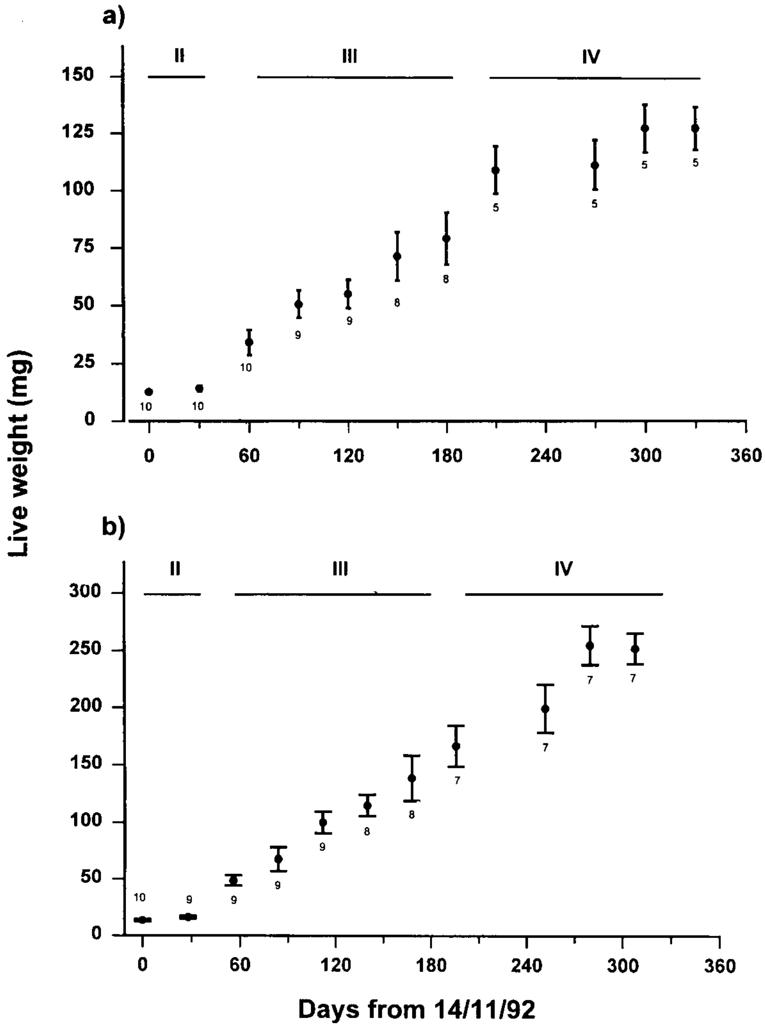


Fig. 3. Mean (± S.E.) monthly live weights (in mg) of *Tipula montana* larvae cultured at 10°C (a) and 15°C (b). The Roman numerals at the top of each graph indicate instar. The number of larvae is given for each data point.

That instar IV larvae did not show any effect with increasing temperature could be that individuals had reached the maximum larval weight (Todd, 1993), and were anticipating the correct photoperiod stimulus for the onset of pupation. Therefore, no significant increase in weight was evident. Growth rates in instar IV larvae of *Tipula subnodicornis* at 7, 10, 15 and 20°C were all very similar (Butterfield, 1976). Indeed, there was a lower growth rate at the highest temperature (20°C) in the largest larvae. When *T. subnodicornis* larvae reach maximum weight they become sensitive to photoperiod and there is some evidence to suggest that during this period the development rate is negatively correlated with temperature.

The fact that temperature had no significant effect on the weight at which moults occurred, means that temperature cannot alter the circumstances under which this change occurs. A larva has to be at a certain weight for a moult to occur and so the temperature has to be high enough to enable a larva in each stage to reach that weight for development to proceed, i.e. there is a size threshold at moulting. Nijhout (1975) also found a size threshold in the lepidopteran *Manduca sexta*: larvae of this insect had to attain a certain head capsule size (5.1 mm) in order for pupation to occur and this was independent on the prior growth history of the larvae. Increasing the temperature only has the effect of accelerating the larval development towards moult. This allows larvae to reach the critical weight for moulting earlier, rather than affecting the weight at which the moult occurs, as larvae did not moult at significantly lower weights at higher temperatures. Stamp & Bowers (1994) found the same situation in larvae of *Spilosoma congrua* as differing temperatures did not have an appreciable effect on their final weight.

The temperature of 1°C was obviously not adequate for any change of instar to occur. 5°C, however, appeared to be adequate for larvae to moult from instar II to III (if at an appropriate weight for the moult to occur) but further development was arrested. A larva in instar III at 5°C would have to reach ca. 45 mg in order for the moult into instar IV to occur. An instar IV larvae would have to reach ca. 115 mg for pupation to occur. These weight thresholds obviously could not be reached by larvae growing at 5°C but were attained by larvae growing at 10 and 15°C. Therefore, the development of larvae of *T. montana* appears to be arrested at low temperatures.

From these results, a minimum temperature of between 5 and 7°C is required both for significant growth to occur throughout the four larval instars, and for all moults to occur successfully in *T. montana*. There was no growth at 5°C and a relatively high growth rate at 7°C. This sudden increase in growth rates at these low temperatures suggests that the temperature threshold in these insects appears to be much lower than in most insects but could be considered typical for insects inhabiting cool environments such as the northern temperate zone. For example, Davies & Ratcliffe (1994) found that larval growth in the blowfly *Calliphora vicina* occurred down to at least 4°C, and pupal formation, development and adult emergence to 5°C. The relevant mean monthly temperature at Waskerley Common is > 7°C for the months of May (7.7°C) to October (7.1°C), rising to a maximum of 12.5°C in July (Jennings, 1982). Therefore, the temperature at which significant growth has been found to occur here (7°C) in *Tipula montana* is the minimum mean monthly temperature during the main growing season at Waskerley Common. From November to May there would be negligible growth of *T. montana*, but as shown above, there will be considerable increase in weight once the temperature reaches 7°C.

At Waskerley, *Tipula montana* follows either a one- or two-year life-cycle (Todd, 1993). In the one-year life-cycle, pupation is dependent upon instar IV larvae attaining an appropriate weight in June/July, for an emergence to occur in late July/August; whereas in the two-year life-cycle, this is dependent upon a photoperiodic stimulus in April/May. If low temperatures are prevalent in particular years (i.e. < 7°C), larvae may be unable to reach the required weight for pupation in June/July and therefore would transfer to the two-year life-cycle, with the adults emerging in early June the following year. This could cause yearly fluctuations in the number of individuals following the two life-cycles, and result in varying numbers of adults produced at each emergence.

So, growth in the larval stages of *Tipula montana* is limited by low temperatures, as growth is severely restricted at temperatures of 5°C and below, and from this study a temperature of at least 7°C was required for successful development of the larval stages to occur.

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