



## BEHAVIOURAL OPTIMIZATION OF BODY TEMPERATURE BY NYMPHAL GRASSHOPPERS (*MELANOPLUS SANGUINIPES*, ORTHOPTERA: ACRIDIDAE) IN TEMPERATURE GRADIENTS ESTABLISHED USING INCANDESCENT BULBS

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**Abstract**—1. Body temperatures ( $T_b$ ) of *Melanoplus sanguinipes* F. nymphs were measured in temperature gradients established using incandescent light bulbs.

2. Relative frequency distributions of possible  $T_b$  were estimated by linking equations describing the effects of distance from the light bulb and orientation to it.

3. The distribution of  $T_b$  was significantly different from that expected if insects positioned themselves randomly, and  $35 \leq T_b \leq 43^\circ\text{C}$  occurred more frequently than expected; this is conclusive evidence for behavioural thermoregulation.

4. The modal  $T_b$ ,  $40^\circ\text{C}$ , approximated the temperatures for maximum rates of feeding ( $38.6^\circ\text{C}$ ) and development ( $42.2^\circ\text{C}$ ); at  $40^\circ\text{C}$ , both rates occur at  $> 95\%$  of their maximum rate. Crown copyright © 1996 Published by Elsevier Science Ltd.

**Key Word Index:** Insect; grasshopper; behaviour; thermoregulation; body temperature; temperature gradient; thermal gradient; optimization; biophysics

### INTRODUCTION

Under natural conditions, body temperatures of diurnal insects are frequently observed to exceed air temperature (Stower and Griffiths, 1966; Anderson *et al.*, 1979; May, 1979; Kemp, 1986). Linear regressions of body temperature on air temperature often have slope  $< 1$  and intercept  $> 0$ ; this result has been interpreted as evidence for thermoregulation, but it is insufficient evidence because in terrestrial ectotherms air temperature is only one of many factors that contribute to body temperature (Stevenson, 1985).

An organism's foraging environment is a spatio-temporally dynamic mosaic of diverse microclimatic factors. At each site, these factors contribute to the potential body temperature of the organism. The organism's orientation to some of these factors further affects the resulting body temperature. Thus, within this environment, there is a range of possible body temperatures, which varies over space and time,

and typically differs from air temperature. Consequently, one plausible explanation for the observed elevation of body temperature over air temperature is that it reflects the net effects of these factors on insects distributed randomly within their environment. The slope of  $< 1$  in a regression of body temperature on air temperature may simply mean that air temperature is an inappropriate independent variable, and that the resulting error is systematic. Similar criticism applies to nonlinear empirical comparisons of body temperature to air temperature.

To demonstrate that thermoregulation is occurring, it is further necessary to demonstrate that the relative frequency distribution of observed body temperatures differs from that of possible body temperatures (Hertz *et al.*, 1993). Therefore, these two distributions must be quantified and compared. Under field conditions this comparison may not be feasible, because of the difficulties in measuring both actual and possible body temperatures. An alternative is to observe insect behaviour, body temperature, and the range of possible body temperatures in simplified model systems, such as thermal gradients.

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Results obtained in these systems may then be used to generate testable hypotheses of insect behaviour under field conditions.

This study was conducted in thermal gradients established using incandescent light sources, and was intended to test whether the nymphs of *Melanoplus sanguinipes* actively thermoregulate and, if so, to determine whether they demonstrate a temperature preference.

#### MATERIALS AND METHODS

Experiments were conducted using temperature gradients established in a 40 × 40 × 40 cm cage that had aluminum sides and back (0.75 mm thick), clear plexiglass front and top (6.75 mm thick), and a corrugated cardboard floor (3.5 mm thick). One circular ventilation port (10 cm diameter) was cut in each of the two side walls, centred 8.5 cm above the floor and covered with 2 mm mesh metal screen. The floor of the cage was covered by tightly-fitted cotton cloth to provide traction. Temperature gradients were established using incandescent bulbs of 3 wattages (25, 40 or 60 W) mounted through a 6 cm diameter opening in the centre of the floor, with its equator coplanar with the floor.

All experiments used fourth and fifth instar grasshoppers (*Melanoplus sanguinipes* F. [Orthoptera: Acrididae]), obtained from a laboratory colony (N = 95). Insects were introduced into the thermal gradients by releasing or restraining them on the floor. Mean insect mass was 184.4 mg (S.D. = 70.3), and mean length was 16.9 mm (S.D. = 3.2).

#### *Temperatures achieved by free-ranging grasshoppers*

In the primary experiment, grasshoppers were released in the cage near the illuminated light bulb and allowed to move freely within the cage until they had adopted relatively constant positions, and their body temperatures had stabilized ( $\approx 10$  min). The temperature reading at the end of this period (terminal temperature) was used as the body temperature measurement. Four grasshoppers were used in each trial; normally, all were exposed to each bulb wattage once but in one trial each grasshopper was exposed to each bulb wattage twice. There was no evident difference in insect response between the two exposures. Bulb wattages were presented in random order.

Insect body temperatures were monitored using copper-constantan thermocouples (0.127 mm diameter, part number SSC-TT-T-36-36, Omega Scientific, Stamford CT, USA), inserted  $\approx 2$  mm into the thorax through an incision between the right meso- and meta-sternites. In this trial, the embedded

thermocouples were fastened in place using adhesive from a hot-glue gun (Mastercraft<sup>®</sup>, model LR63745). Insect body temperatures were recorded to 0.01°C every 10 sec using a data logger (Model 21X, Campbell Scientific, Edmonton, AB, Canada).

The bulb was turned off and the insects were allowed to return to room temperature ( $\approx 22^\circ\text{C}$ ) over a period of  $\approx 10$  min. The bulb was changed, and the heating and cooling process was repeated. After each trial, insects were weighed (fresh weight) to 0.1 mg and their length (frons to the posterior tip of the abdomen) was measured to 0.1 mm using a hand-held micrometer (Manostat<sup>®</sup>). Regression was used to test for any relationship between body size and final body temperature.

#### *Estimation of possible body temperatures*

Exhaustive census of the frequency distribution of possible temperatures was impractical, and so a modelling approach was adopted. Two variables affected each insect's body temperature: its distance from the lightbulb source and its orientation to the lightbulb. Equations were derived describing the effects of each variable, then linked to estimate the relative frequency distribution of possible body temperatures in the gradients.

In these trials, the insects were fastened to small pieces of cork ( $\approx 2 \times 2 \times 3$  mm) using upholstery glue (EC2218<sup>®</sup>, 3M Co., Ltd.). Their hind legs were glued to their abdomens using the same glue. Each small cork piece was transfixed by an insect pin, with its head against the insect's thoracic sternites. The insect pin was pushed entirely through the floor so that the bottom of the cork and the insect's tarsi contacted the substrate. Body temperature was monitored using embedded thermocouples as described above.

*Distance effects.* The effect of distance from the light bulb on insect body temperatures was measured by restraining nymphs in known orientations at specified distances from the light bulbs. A cartesian (x,y) coordinate system was established, with the origin at the centre of the lightbulb and the axes parallel to the walls of the cage. Eight transects were defined radiating from the centre of the lightbulb, four on the cartesian axes and four on the diagonals. On the transects along the axes, insects were placed at 5, 10 and 15 cm from the centre of the bulb for wattages 25 and 40; for the 60 W bulbs, the minimum distance was 7.5 cm because the insects died at 5 cm. On the diagonal transects the same x- and y-coordinates were used; consequently the distances of these insects from the bulb centre were  $\sqrt{2}$  times the distances along the axes. These transects resulted in a total of six distances from the centre of the

lightbulb, with four replicates at each distance for each wattage.

One nymph was used on each transect, and was presented in two orientations to the bulb in each position: face on (yaw angle = 0°) or broadside (yaw angle = 90°). For each nymph, distances from the bulb were assigned randomly, as were orientations within distance.

In each case, the lightbulb was turned on and grasshopper body temperatures were monitored for 10 to 15 min. The bulb was then turned off and the insect was allowed to cool to room temperature for ≈ 10 min. The insect was then moved or reoriented and the heating and cooling cycle was repeated.

*Orientation effects.* The effect of orientation to the bulb on body temperature was examined by restraining grasshoppers at a range of distances from a 40 W bulb, and presenting each at 0, 30, 45, 60 and 90° yaw angles to the bulb. Two trials were performed; in each, one insect was placed on each of the eight transects at one of the x,y positions used in the previous trials, randomly chosen. The insects were subjected to cycles of heating and cooling as in the temperature-surface characterization trial, except that all heating periods lasted 15 min. Orientation was varied randomly for each insect.

#### ANALYSIS OF THESE TRIALS

##### *Body temperatures.*

Body temperatures of the restrained insects approached the final value asymptotically. Because this type of curve takes an infinite amount of time to attain the final value, time constraints became important. Consequently, temperature data were analyzed by applying Newton's law of cooling, in which the rate of change of body temperature is directly proportional to the difference between the current value and an asymptotic value (Equation [1]).

$$\frac{T_b(t) - T_b(\infty)}{T_b(0) - T_b(\infty)} = \exp(-a \cdot t), \quad (1)$$

where  $T_b(t)$  is body temperature at some specified time after the initial measurement ( $t = 0$ ),  $a$  is a rate parameter and  $T_b(\infty)$  is the asymptote, i.e. the body temperature the insect would have attained if allowed infinite time to equilibrate. Equation [1] was rearranged to isolate  $T_b(t)$  and used to estimate values of  $a$  and  $T_b(\infty)$  by iterative nonlinear regression (PROC NLIN, Marquardt algorithm, SAS Institute, 1990). All subsequent analyses represented body temperature by  $T_b(\infty)$ .

##### *Distance effects*

At each orientation to the bulb, the decrease in insect temperature with distance conformed to an asymptotic inverse-square relationship:

$$T_b(X) = b \cdot X^{-2} + c \quad (2)$$

where  $X$  is the distance of the insect from the bulb,  $b$  is the temperature of an insect 1 cm from the centre of the bulb, and  $c$  is the temperature of an insect at an arbitrarily great distance from the centre of the bulb. Parameters were estimated by linear regression.

##### *Orientation effects*

Temperatures of insects at various orientations ( $\theta$ ) to the bulb fell between temperatures of insects at 0 and 90° according to a relationship of the form:

$$\frac{T_b(\theta^\circ) - T_b(0^\circ)}{T_b(90^\circ) - T_b(0^\circ)} = d \cdot \sin|\theta| \quad (3)$$

The absolute value was used to avoid artefactual cooling effects at negative angles, for which  $\sin \theta < 0$ . The value of  $d$  was estimated by linear regression.

##### *Test of body temperature estimation model*

Equations [2] and [3] comprise a model to estimate the body temperature of an insect at any combination of orientation and location in the cage, for each bulb wattage. These modelled temperatures were tested by comparing them to observed temperatures of insects at specified locations in the temperature gradients. In these trials, the floor of the cage was covered by graph paper.

Grasshopper nymphs without thermocouples were released in the cage. The bulb was turned on and the insects were left for 10 to 15 min to adopt a steady position relative to the bulb. Three sets of grasshoppers were used, each at all three bulb wattages. The sets consisted of 25, 43, and 41 grasshoppers, respectively.

After the insects had adopted steady positions, the cage was photographed from above using a Sinar P2 camera, which produces 10 × 12 cm negatives. The coordinates of the head and tail of each insect were read from the negatives. Distances of the grasshoppers from the centre of the bulb, and their orientation to the bulb were obtained from these coordinates. Body temperatures were modelled using equations [2] and [3].

To test the modelled body temperatures, two trials were conducted in which grasshoppers were restrained, using the pinned cork pieces described earlier, in positions adopted by the free-ranging grasshoppers in the photographs. Most free-ranging grasshoppers adopted final positions within a ring around the lightbulb, and many were partially shaded

by their neighbours. When measuring body temperatures of the restrained insects we ensured that they were shaded in the same manner as the grasshoppers in the photographs, by restraining 10 grasshoppers in the positions occupied by free-ranging grasshoppers which had adopted adjacent positions in the rings, and measuring body temperatures for all but the two on the ends.

These trials used grasshopper position data from the photographs taken for the third free-range trial. In the test at 60 W, temperatures were measured for all grasshoppers; at other wattages, temperatures were measured for 32 grasshoppers in four separate clusters of eight (i.e. 10, less the two on the ends). For each such grasshopper, body temperature was followed over time and the asymptotic temperature value was estimated using equation [1]. Modelled temperatures were compared to observed temperatures by linear regression.

#### *Frequency distribution of possible body temperatures*

The frequency distribution of possible body temperatures was approximated by estimating body temperatures of hypothetical grasshoppers on a grid with (x,y) coordinates every 0.5 cm, discarding locations within the light bulb. For each bulb wattage, body temperatures were estimated using equation [2] for insects at angles of 0 and 90°, then equation [3] was used to interpolate body temperatures on 5°C increments. Output temperatures were rounded to 1°C and a relative frequency distribution was compiled.

#### *Relative preference of the insects for specific body temperatures*

The relative frequency distributions of observed insect body temperatures were compared to those of possible body temperatures. At each bulb wattage, the relative occurrence index (ROI) for the free-roaming grasshoppers with embedded thermocouples was

determined by dividing the relative frequency at which insects occurred at specified temperatures, by the frequency at which those temperatures were calculated to occur. Where ROI > 1, the grasshoppers occur more frequently than expected at random.

## RESULTS AND DISCUSSION

### *Temperatures achieved by grasshoppers*

After the lightbulb was turned on, insect body temperatures increased, generally to  $\approx 40^\circ\text{C}$ , then stabilized due to the insects' behavioural responses. Thereafter, each insect's body temperature remained relatively constant. A few insects settled at lower body temperatures than did most other nymphs, particularly in gradients established using 25 W light bulbs.

Terminal body temperature varied within and among insects. It did not differ significantly among insects over bulb wattages (ANOVA,  $P(>F) > 0.35$ ); it was not affected significantly by bulb wattage (ANOVA,  $P(>F) > 0.3$ ) nor by insect size (mass or length), either as a main effect or as an interaction with bulb wattage (ANOVA,  $P(>F) > 0.6$ ).

Linear regressions of terminal temperature on insect size were not significant whether size was represented by mass ( $F_{1,14} = 0.28$ ,  $P(>F) = 0.6$ ,  $r^2 = 0.0195$ ) or by length ( $F_{1,14} = 0.43$ ,  $P(>F) = 0.5$ ,  $r^2 = 0.0300$ ). Evidently, thermoregulatory behaviour balances the opposing effects of convective cooling and radiative heating on body temperature despite their different importance with changing size (Digby, 1955; Church, 1960; Lactin and Johnson, 1996; Lactin and Johnson, submitted; Stevenson, 1985).

### *Estimation of possible body temperatures*

*Distance effects.* Parameter estimates for equation [2] are given in Table 1 for each bulb wattage and insect orientation. The estimates of parameter b

Table 1. Parameters of equation [2], describing decrease in body temperature with distance from light bulbs of three wattages, for insects facing the lightbulb (0°) and broadside to it (90°).

| Orientation<br>Angle (°) | Parameter |       |      |      |           |        |
|--------------------------|-----------|-------|------|------|-----------|--------|
|                          | b         |       | c    |      | $F_{2,5}$ | $r^2$  |
|                          | Est.      | S.E.  | Est. | S.E. |           |        |
|                          | 25W Bulb  |       |      |      |           |        |
| 0                        | 246.5     | 11.5  | 29.1 | 0.2  | 25845.7   | 0.9893 |
| 90                       | 374.3     | 12.3  | 28.9 | 0.2  | 22480.3   | 0.9957 |
|                          | 40W Bulb  |       |      |      |           |        |
| 0                        | 296.6     | 13.0  | 31.6 | 0.2  | 23285.7   | 0.9924 |
| 90                       | 413.4     | 46.0  | 31.1 | 0.8  | 1990.2    | 0.9528 |
|                          | 60W Bulb  |       |      |      |           |        |
| 0                        | 630.8     | 151.1 | 31.8 | 1.4  | 1224.8    | 0.8134 |
| 90                       | 825.4     | 139.9 | 33.8 | 1.3  | 1921.7    | 0.8969 |

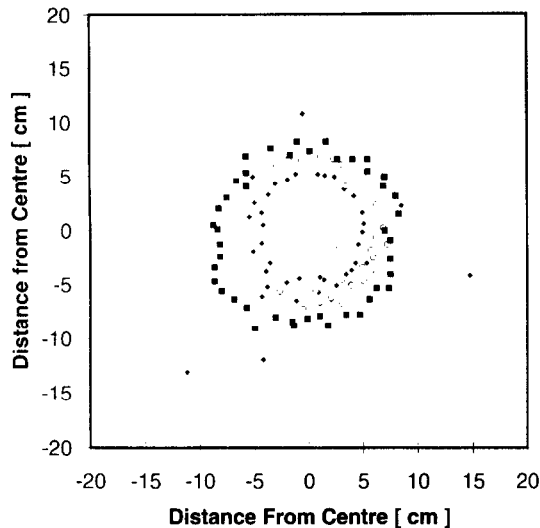


Fig. 1. Final positions of free-roaming *M. sanguinipes* nymphs in three temperature gradients, by lightbulb wattage: ◆, 25W; ○, 40W; ■, 60W. Symbols are placed at the centre of the nymph.

increased with both bulb wattage and orientation angle. Estimates of parameter *c* also increased with bulb wattage, but the change with orientation was not consistent. Where 25 and 40 W bulbs were used, *c* was slightly ( $\leq 0.5^{\circ}\text{C}$ ) greater at  $0^{\circ}$  than at  $90^{\circ}$  yaw, suggesting that at greater distances, the insect would be slightly cooler when broadside to the bulb than when face-on. We attribute these results to random variation. In all cases at such distances the effects of orientation change are minimal.

**Orientation effects.** The estimate of parameter *d* from equation [3] was  $1.04 \pm 0.066$  ( $F_{1,9} = 239.5$ ,  $P(> F) \leq 0.0001$ ,  $r^2 = 0.9638$ ). The value of *d* is not significantly different from 1.

The effects of distance and orientation were both consistent with body temperature elevation being due entirely to the amount of energy intercepted. The inverse square relationship of body temperature to distance was consistent with the decrease in apparent luminosity of a light source with increasing distance. Similarly, the change in body temperature of restrained insects with orientation to the light source was consistent with the change in the amount of energy intercepted.

#### Test of body temperature estimation model

In each photographed trial, the insects distributed themselves around the bulb in a ring, the radius of which increased with bulb wattage. Figure 1 illustrates the results of one trial. In most cases, a few insects occurred at greater distances from the lightbulb than did most other insects in the same trial.

Regressions of observed temperatures on modelled temperatures were highly significant. For individual observed/modelled pairs, intercept =  $3.64 \pm 7.12$ ; slope =  $0.89 \pm 0.17$  ( $F_{1,87} = 27.3$ ,  $P(> F) \leq 0.0001$ ,  $r^2 = 0.2385$ ). Where modelled temperatures were rounded to classes of  $1^{\circ}\text{C}$  and regressions were performed using mean observed temperatures in each class, weighted by the number of observations per class, intercept =  $-1.32 \pm 10.4$ ; slope =  $1.01 \pm 0.25$  ( $F_{1,11} = 16.7$ ,  $P(> F) = 0.0018$ ,  $r^2 = 0.6030$ ). In both regressions, the intercept was not significantly different from 0 and the slope was significantly  $> 0$  but not significantly different from 1, indicating that the modelled and observed temperatures are scattered around the 1:1 line representing perfect agreement. However, at each modelled temperature, there was a considerable range of observed temperatures (i.e. in the temperatures of insects restrained in positions adopted by free-ranging insects). This range reflects the distribution of individuals around the mean body temperature, particularly those which adopted positions conspicuously farther from the light bulb than most insect in the same trial. This range of body temperatures probably results from stochastic or imperfect optimization behaviour (Fig. 2).

The effect of this variation was particularly apparent where regressions were performed using individual observations. Nonetheless, the performance of the model is reasonable in predicting individual body temperatures, and when used to predict mean temperatures of a group of insects, it performs well.

#### Frequency distribution of possible body temperatures

At each bulb wattage, the relative frequency distribution of possible temperatures, as modelled using equations [2] and [3], was unimodal with a skew towards high temperatures (Fig. 3). The modal temperature was 31, 32 and  $35^{\circ}\text{C}$  for bulb wattages 25, 40 and 60, respectively.

Figure 3 also includes the relative frequency distribution of the observed body temperatures at each bulb wattage. In all cases, the mean of this distribution was significantly higher than that of possible temperatures (one-tailed *t*-test,  $P(> t) < 0.05$ ). Thus we rejected the null hypothesis that the distribution of body temperatures is equivalent to that expected at random and concluded that the insects were actively thermoregulating.

#### Relative occurrence of the insects at specified temperatures

Figure 4a illustrates the distribution of the relative frequency of observed insect body temperatures, pooled over trials and bulb wattages. The distribution

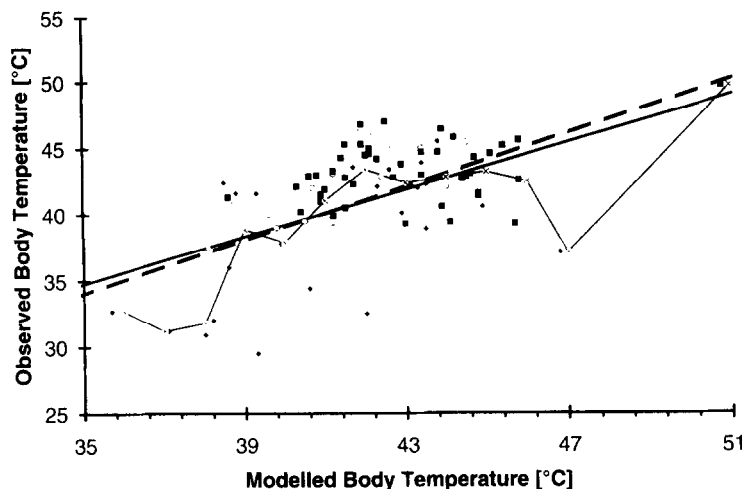


Fig. 2. Body temperatures of free-roaming *M. sanguinipes* nymphs in three temperature gradients, modelled using equations [2] and [3] in the text, plotted against measured temperatures. Symbols: ◆, 25 W light bulbs; ○, 40 W; ■, 60 W; x joined by fine line, mean observed temperatures in classes of modelled temperature (rounded to 1°); solid line, regression of individual observed body temperatures on predictions; broken line, regression of class mean observed temperature on rounded modelled temperature, weighted by number of observations in class.

of body temperatures was unimodal with a peak at 40°C and a skew toward lower temperatures. Chapman (1955) obtained the same result with nymphs of the migratory locust, *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae), and Vuillaume

(1954) observed that nymphal *Zonocerus variegatus* (L.) (Orthoptera: Acrididae) always congregated between 36 and 40°C. However, neither author measured body temperatures directly, but instead assumed that it was the same as air or surface temperature at the location on the gradient. This assumption is questionable because grasshoppers can affect their body temperature by adjusting either the area of contact between their body and the heated surface, or the elevation of their body above it (Anderson *et al.*, 1979) and therefore it is not certain that the temperatures given actually represent body temperature. Further, neither corrected for the relative frequency of possible body temperatures, and thus their data are not convincing evidence for thermoregulation.

Figure 4b illustrates that the distribution of the ROI was also unimodal with a peak at 40°C and a slight skew toward lower temperatures. Insect body temperatures in the range 35°–43°C occurred more frequently than expected at random.

Within the cages, other gradients probably occurred (e.g. light intensity and relative humidity) which were correlated with the temperature gradient, and the possibility exists that the insects responded to these other gradients rather than to temperature. The use of light bulbs of three wattages was intended to allow a test of this possibility. The mean and range of body temperatures were practically the same at all bulb wattages; for this result to occur as a consequence of a response to some other factor(s) would be an unlikely coincidence. The most parsimonious explanation is that the insects responded to

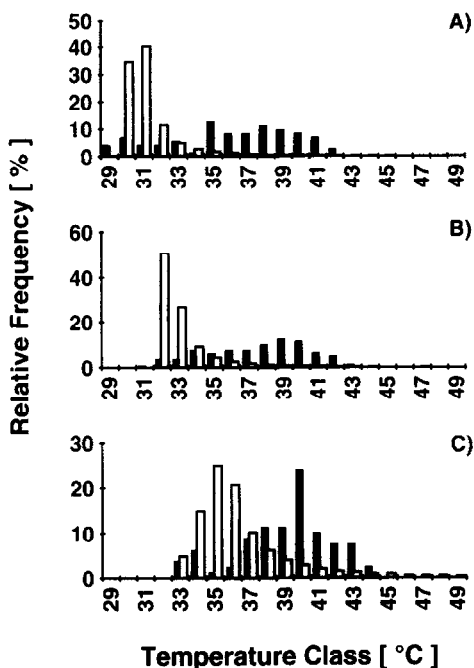


Fig. 3. Observed relative frequency distributions of measured body temperatures of free-roaming *M. sanguinipes* nymphs in three temperature gradients (solid bars) and the distribution of possible body temperatures, as modelled using equations [2] and [3] in the text (open bars). A) 25 W lightbulb; B) 40 W lightbulb; C) 60 W lightbulb.

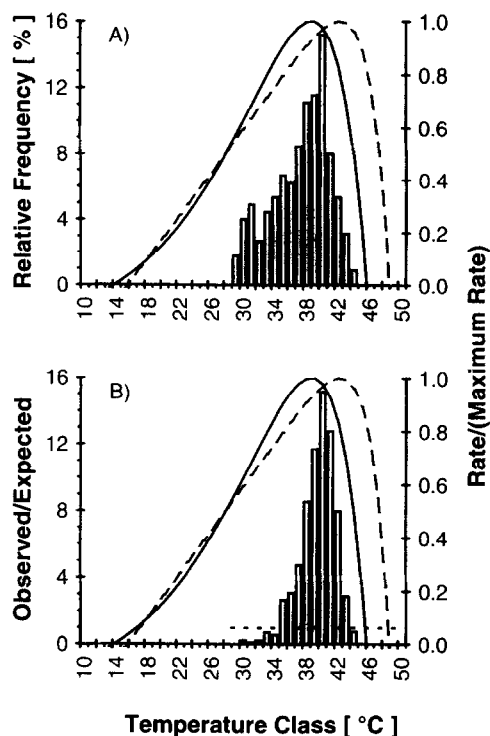


Fig. 4. Distributions of *M. sanguinipes* nymphs, allowed to position themselves in a temperature gradient, pooled over lightbulb wattages (left ordinate). The curves describe the temperature-dependence of feeding by fifth instars (solid curve), and of the developmental rate over the nymphal stage (broken curve). Each curve is scaled to a proportion of the maximum rate (right ordinate). A) Observed relative frequency distributions of body temperatures. B) Relative occurrence index (ROI) of body temperatures, i.e. observed relative frequency of body temperature, divided by relative frequency at which temperature is possible in the gradient. Horizontal broken line, ROI = 1 (restricted to range of possible temperatures). Where ROI > 1, body temperatures occur more frequently than expected if insect distribution is random.

temperature. Thus, our results constitute strong evidence for thermoregulation by these nymphs.

Figure 4a and b also include curves representing the temperature-dependence of feeding for fifth instars (Lactin and Johnson, 1995) and of development through the entire nymphal stage (Lactin *et al.*, 1995, using data from a literature review by Hilbert and Logan, 1983), with each function scaled to a proportion of the maximum value; 40°C is very near the temperature for maximum feeding (38.6°C) and development (42.2°C). At 40°C, both rates occur at > 95% of their maximum value.

Thus, in addition to elevating body temperature over that expected if insects distributed themselves at random within the thermal gradient, the behavioural responses of the insects resulted in a distribution of body temperatures which had a mode close to the temperatures at which feeding and development

are greatest, and a narrow distribution around this mode.

The body temperature of field-active terrestrial ectotherms frequently approximates the optimum for one or more ecologically-important physiological processes; by maintaining this temperature, the organisms accrue numerous advantages (Huey and Kingsolver, 1989). The results of this study suggest that at least in this species, thermoregulatory behaviour results in maintenance of body temperature near the optimum for development and feeding, and perhaps other processes. One obvious advantage of this behaviour is that developmental time is minimized.

These results are conclusive evidence for active thermoregulation in nymphs of this species, and for existence of a preferred temperature near 40°C. Although these results were obtained in the laboratory, grasshoppers in nature behave in ways which are plausibly explained as thermoregulatory responses (Uvarov, 1977), and we believe that in nature these responses would also result in body temperatures near 40°C where this is possible.

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