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Response of body temperature to solar radiation in restrained nymphal migratory grasshoppers (Orthoptera: Acrididae): influences of orientation and body size

DEREK J. LACTIN and DAN L. JOHNSON Land Resource Sciences Section, Research Centre, Agriculture and Agri-Food Canada, and Department of Geography, University of Lethbridge, Lethbridge, Canada

Abstract. We restrained forty-nine nymphal migratory grasshoppers (*Melanoplus sanguinipes*) in a series of orientations to the sun and measured rate of temperature change due to radiation intercepted, compensating for temperature loss by convection and greybody reradiation. Direct solar radiation affected body temperature significantly, but diffuse radiation did not. The coefficient of direct solar heating (H_{dir}), varied from 0.603 to 0.690 depending on how radiation interception was estimated, and on whether insect size was expressed as mass or as a function of length. H_{dir} is the rate of temperature change as a proportion of the maximum rate assuming complete conversion of all incident radiation to heat. None of the H_{dir} estimates was significantly different from visible-spectrum absorbance to (0.722), suggesting that the latter is a reasonable approximation of H_{dir}.

In simulations, equilibrium body temperature elevation decreased with body size where energy influx was expressed as the amount intercepted (*W*), but increased with body size when expressed as insolation as ($W \cdot m^{-2}$) because at a specified insolation, the amount of energy intercepted increases with body size. Expressing energy influx as the amount intercepted reveals the underlying biophysical mechanisms which determine body temperature.

This paper presents a model of body temperature elevation in which fundamental physical processes are assembled to provide good estimates. This basis in physics implies that the model can can be applied with confidence to conditions other than those in which it was derived.

Key words. *Melanoplus sanguinipes*, grasshopper, thermoregulation, body temperature, biophysics, solar radiation, insolation, convection, greybody radiation, simulation model.

Introduction

Among ectothermic insects, many ecologically important processes proceed at rates which depend on body temperature; these include development, fecundity, mortality and feeding (Messenger, 1964; Hagstrum & Leach, 1973; Welbers, 1975; Walgenbach & Wyman, 1984; Lamb & Gerber, 1985; Ferro *et al.*, 1985; Logan *et al.*, 1985; Groden & Casagrande, 1986; Elliot & Kiekhefer, 1989; Lactin & Holliday, 1993; Lactin *et al.*, 1993; Lactin & Johnson, 1995).

The temperature of any object is determined by the rates at which it gains and loses energy. By responding to environmental heterogeneity (behavioural thermoregulation), many terrestrial ectotherms can control their body temperature by affecting rates of energy gain and loss (May, 1982; Huey & Kingsolver, 1989). For terrestrial ectotherms of mass <1 g, solar radiation is the most important factor contributing to elevation of body temperature above air temperature (Stevenson, 1985). Many insects can influence the amount of radiation intercepted by changing their orientation to the sun (e.g. May, 1976; Anderson *et al.*, 1979). As a result of this behavioural response, the realized relationship between body temperature and air temperature is not linear. In grasshoppers of several species under field conditions, body temperature elevation above air temperature was well described

Correspondence: Dr Derek J. Lactin, Land Resource Sciences Section, Research Centre, Agriculture and Agri-Food Canada, Box 3000, Lethbridge AB, Canada T1J 4B1.

by a logistic curve with an asymptote at *c.* 42°C (Kemp, 1986). Body temperature of *Camnula pellucida* (Orthoptera: Acrididae) changes in a nonlinear manner under combined variation in air temperature and solar radiation, with a maximum at *c.* 42°C (Carruthers *et al.*, 1992).

Behavioural thermoregulation has important economic, ecological and biogeographic consequences. Usually, the resulting body temperature exceeds air temperature (Heinrich, 1977) and frequently approximates the optimum for one or more temperature-dependent processes (Huey & Kingsolver, 1989). In laboratory temperature gradients, *Melanoplus sanguinipes* (Orthoptera: Acrididae) nymphs maintain body temperatures near the optima for feeding and development (Lactin & Johnson, 1996a). Under field conditions these responses would both accelerate phenology and increase potential damage to crops and rangeland, relative to non-thermoregulating insects. Further, solar heating may be necessary for local insect populations to complete one generation per year (Carruthers *et al.*, 1992); this result suggests that thermoregulation may help determine the geoclimatic limits to species distributions. Therefore a detailed understanding of the process will have wide application in economic and ecological entomology.

Kemp (1986) and Carruthers *et al.* (1992) have derived equations which describe equilibrium body temperature elevation of grasshoppers under specified conditions. However, because empirical equations of the type derived by these authors describe responses under a specific set of conditions, they are inherently retrospective and potentially site-specific; consequently their applicability to other situations is not clear. Our aim is to develop a mechanistic model of behavioural thermoregulation by characterizing and assembling equations describing the responses of the insects' body temperature to component physical influences. Being based on fundamental physical principles, this model will be transportable to novel conditions.

Materials and Methods

Experimentation

Live *M.sanguinipes* nymphs of instars 3–5 were restrained in known orientations to the sun under field conditions and their internal thoracic temperature was monitored. Levels of solar radiation were created by shading, and the orientation of the insects was varied with respect to the solar vector (i.e. a line from the insect to the sun). Energy intercepted by each insect was calculated from solar radiation and the insect's orientation and dimensions.

The experiment was conducted at Lethbridge, Alberta, Canada (49.7°N, 112.8°W) in an open field of crested wheat grass, *Agropyron cristatum*; canopy height was *c.* 0.2 m. Insects used were either field-collected or reared from a non-diapause laboratory strain. Nymphs of the non-diapause strain are conspicuously darker than those collected from the field.

The insects were mounted and presented to the sun on an experimental device which consisted of two planks (60 × 15 × 1.5 cm) with the long axes connected by hinges. Six pivots were mounted perpendicular to the upper plank, and one size 14 cork stopper was mounted upright on each pivot. The device was set, with the hinges away from the sun, at 0.7 m above the ground on a portable table (0.6 × 0.8 m). The device was levelled and mounted with its long axis perpendicular to the solar vector. Thereafter the upper plank was adjusted to match the elevation angle of the sun. About every 15 min during the experiments the orientations of the long axis and the upper plank were adjusted to remain perpendicular to the solar vector and parallel to the solar elevation angle, respectively.

Each nymph was restrained by attaching a piece of cork (2 × 2 × 3 mm) to its thoracic sternites using glue (EC2218, 3M® Co. Ltd., London, Ontario, Canada). The cork piece was attached by an insect pin to one of the cork stoppers on the experimental device. One nymph was mounted on each cork. The insects' hind legs were immobilized by gluing them to the abdomen with the same adhesive.

Orientation of the insects to the sun was adjusted by rotating the corks on the pivots. Orientation was varied independently in 30° increments around one of three axes: the *x*-axis passed from the centre of the insect to the sun; the *y*-axis was horizontal and perpendicular to the *x*-axis; and the *z*-axis was perpendicular to both. Yaw was defined as rotation around the *z*-axis, and pitch as rotation around the *y*-axis. Roll was defined as rotation around the long axis of the insect (i.e. a line segment joining the frons and tail), regardless of the yaw and pitch angles. For yaw manipulations, the angles were from 0° (long axis parallel to solar vector, with frons toward the sun) to 90° (long axis perpendicular to solar vector). For pitch, the angles were 0° (long axis parallel to solar vector, with frons toward the sun) through 90° (long axis perpendicular to solar vector, with dorsum towards the sun) to 180° (long axis parallel to the solar vector, with frons away from the sun). Roll angles were 0° (dorsoventral axis perpendicular to the solar vector) to 90° (dorsoventral axis parallel to the solar vector, with the dorsum toward the sun). For yaw manipulations, roll and pitch were fixed at 90° and 0°, respectively. For pitch manipulations, roll and yaw were fixed at 90° and 0°, respectively. For roll manipulations, yaw and pitch were fixed at 90° and 0°, respectively.

Levels of solar radiation were obtained using 0, 1, 2 or 4 layers of 42 mesh cm^{-2} black nylon window screen, on a frame (0.5 × 1 m) set perpendicular to the solar vector at the top of a vertical pole (1.5 m). The screen was 1 m from the insects.

Solar radiation (Watts per [m^2 horizontal surface], i.e. $W \cdot m^{-2}$) can be partitioned into two components, direct (i.e. travelling along or near the solar vector), and diffuse (i.e. reflected off clouds or other objects, or reradiated from the atmosphere) (Porter & Gates, 1969). We examined the effects of direct and diffuse solar radiation separately because the two are spectrally distinct and could be expected *a priori* to have differing effects on body temperature. The components were measured using two silicon pyranometers (Model LI200S, LI-COR Instrument Corp., Lincoln, Nebraska, U.S.A.), mounted with their detector heads horizontal. The pyranometers were mounted at the same level as the insects, and had a clear view of the horizon. During the experiment, both pyranometers were shaded in the same manner as the insects. One pyranometer was configured to receive only diffuse solar radiation by shielding the detector from direct solar radiation using a black shade (37 × 10 mm) on an equatorially-mounted wire ring (90 mm diameter). The second pyranometer was not shielded, and detected total solar radiation. Direct solar radiation was obtained by difference from these two readings.

Wind speed was measured using a spinning-cup anemometer (Model 013A Met-One Inc., Grant's Pass, Oregon, U.S.A.), mounted at a height of 1.4 m, *c.* 2 m west of the mounted insects. The orientation of the insect to the wind does not affect the rate of cooling (Lactin & Johnson, 1997) and so this measurement was disregarded.

Nymphal body temperatures were measured using 0.125 mm diameter copper–constantan, teflon-insulated thermocouples (Omega Inc., Stamford, Connecticut, U.S.A.) which were inserted *c.* 2 mm into the thorax through an incision on the right side. This side was never exposed to direct solar radiation. Body temperature of experimental nymphs was compared with that of a reference nymph restrained at the centre of a small Stevenson screen (0.21 × 0.27 × 0.51 m), *c.* 2 m north of the mounted insects. This nymph was otherwise treated the same as, and mounted at the same height as, the experimental nymphs.

All data were recorded on a datalogger (Model 21X, Campbell Scientific, Edmonton, Alberta, Canada). Readings were taken every 0.5 s and output as means every 12 s. Data were collected for at least 2 min for each combination of insect orientation and shade level.

After each trial, the weight (in grams) and four body measurements (in millimetres) were taken from each insect: length, dorsal breadth across the pronotum, maximum ventral breadth including the bases of the metafemora, and depth. Lengths were measured to 0.5 mm using a hand-held micrometer. The insects were then frozen and stored at –40°C.

Relationships between the five physical measurements were characterized by logarithmic regression. These relationships were used in later simulations of responses of body temperature to environmental variables.

Statistical analyses

Estimates of the effect of solar energy on body temperature under field conditions were made by quantifying the response of body temperature to energy intercepted per unit mass, and the rate at which body temperature changed, allowing for energy loss by convection and greybody (Stefan-Boltzmann) reradiation.

Estimates of energy interception. Direct solar energy intercepted by each grasshopper (*QDIR*) was estimated by multiplying measured direct solar radiation ($W \cdot m^{-2}$) by the area of the shadow cast by the insect on a horizontal surface (A_H, in m^2). Shadow area was used because the pyranometers were configured to measure solar radiation incident on a horizontal surface. This estimate was made by measuring the silhouette area (A_p) of the insect on a plane perpendicular to the solar vector, then converting this to A_H using the relationship $A_H = A_p/\cos(Z)$, where Z is the solar zenith angle, calculated from Julian date, solar time and site latitude (Robertson & Russelo, 1968).

Silhouette area was estimated by two methods. The first estimate (A_H) was obtained using image analysis. This estimate was obtained for the nymphs from half of the trials, randomly chosen. Each of the chosen nymphs was mounted under a video camera in the same axes of rotation and relative angles to the line of sight as it had been oriented to the solar vector in the field trials. The nymphs retained the glue used to restrain them, and so remained in the same position as in the field experiment. Analogue images were acquired at standard magnification through a black-and-white video camera (model Dage 68, DAGE-MTI Inc., Michigan City, Indiana, U.S.A.) and input to an image analyser (model Tracor Northern 8502, Noran Inc., Middleton, Wisconsin, U.S.A.). The analogue images were converted to 512 × 512 pixel digital images and greyscale range of 0 (perfect reflectance) to 255. Two greyscale thresholds were adjusted to isolate the image of the grasshopper, and the number of pixels comprising the image was converted to A_p using an empirically derived calibration constant. The visible-spectrum absorbance of the insect (proportion of incident visible light not reflected) was calculated from the mean reflectance of the pixels comprising the image.

The second estimate of the grasshopper's silhouette area on a plane perpendicular to the solar vector ($\hat{A}_p$) was obtained geometrically, by approximating each grasshopper as a trapezoidal prism. Contributions of the sides and faces to the silhouette were calculated trigonometrically. The relationship between $\hat{A}_p$ and A_p was quantified by regression and a correction equation was derived to account for the bias observed. The corrected value of $\hat{A}_p$ was converted ($\hat{A}_H$) by dividing by cos(Z). This estimate was obtained for all insects used in the trials.

Diffuse solar radiation intercepted by the insect (QDIF) was estimated by multiplying diffuse solar radiation by the estimated surface area (A_s) of the insect. Where area is in square metres and mass (M) is in grams, $A_s = 0.0013 \cdot M^{0.8}$, with $r^2 = 0.9573$ (Lactin & Johnson, 1997).

The solar heating coefficient. Estimation. Assuming that solar radiation is the only source of heat gain, and that convection and greybody reradiation are the only sources of heat loss, body temperature changes over time as a function of the dynamic balance between the gain and loss (1):

$$\frac{Q_{\text{net}}}{dt} = H_{\text{dir}} \cdot \text{QDIR} + H_{\text{dif}} \cdot \text{QDIF} - \Delta T \cdot h_0 \cdot M^{i} \cdot (0.1 + U)^{j} - A_s \cdot \Delta T \cdot \left[4\sigma\varepsilon K_e^3\right] \qquad (1)$$

h_0, = 14.571, i = –0.3798, j = 0.5659, U = wind ($m \cdot s^{-1}$), where the term in square brackets is a linear approximation of the Stefan-Boltzmann law (Bligh & Johnson, 1973; Monteith, 1974) and ε is set at 0.94 (Campbell, 1977).

Equation (1) is not directly applicable to our data because we measured rates of temperature change, as opposed to energy exchange. To convert (1) to a form which expresses temperature change, all quantities are divided by $M \cdot c_p$, where c_p is specific hent capacity, estimated to be $3.63\, J \cdot g^{-1} \cdot {}^\circ C^{-1}$ (Lactin & Johnson, 1997). This gives equation (2):

$$\frac{\partial \Delta T}{\partial t} = H_{\text{dir}} \frac{\text{QDIR}}{M \cdot c_p} + H_{\text{dif}} \frac{\text{QDIF}}{M \cdot c_p} - \Delta T \cdot \left[\frac{h_0 \cdot M^{i} \cdot (0.1 + U)^{j}}{M \cdot c_p} + \frac{A_s \cdot 4\sigma\varepsilon K_e^3}{M \cdot c_p} \right] \qquad (2)$$

For analysis, equation (2) was rearranged to

$$\frac{\partial \Delta T}{12s} + \Delta T \cdot \left[\frac{h_0 \cdot M^{i} \cdot (0.1 + U)^{j} + A_s 4\sigma\varepsilon K^3}{M \cdot c_p} \right] = H_{\text{dir}} \frac{\text{QDIR}}{M \cdot c_p} + H_{\text{dif}} \frac{\text{QDIF}}{M \cdot c_p} \qquad (3)$$

and H_{dir} and H_{dif} were estimated using multiple linear regression. In the following presentation, the dependent variable (the left-hand side of equation (2)) is referred to as 'CHANGE.' Both sides of equation (3) have units of °C·s⁻¹; therefore, H_{dir} and H_{dif} are dimensionless constants which express the observed rate of temperature change as a proportion of the maximum rate attainable if all incident energy were intercepted and converted to temperature change.

Analyses were performed on means by trial, insect, shade level, orientation and, where appropriate, axis of rotation, weighted by the number of observations per mean. This approach reduced the variance attributable to temporal variation in air temperature and the limited resolution of the anemometer.

Experimental variables, such as the effects of trial, insect, the absorbance of the insect and axis of rotation are overlain on the basic relationship in equation (2). Therefore an initial analysis of variance was performed which quantified the effects of each of these factors plus all two-way interactions. Trial and insect nested within trial were considered random effects, and the appropriate error terms were used in the F-tests.

Subsequently, H_{dir} was estimated by multiple linear regression. (The effect of diffuse solar radiation was not significant.) Because the regressions treat the observations as if independent, they use an error degrees of freedom (*dfe*) based on the number of observations (N_{obs}). However, the observations are actually repeated measures on a smaller number of insects (N_{ins}). Therefore, where appropriate, standard errors and statistical tests were recalculated using N_{ins} as *dfe*.

Four estimates of H_{dir} were obtained. Two were obtained using A_s as obtained using image analysis, and two used the geometric estimate $\hat{A}_s$. For both A_s and $\hat{A}_s$, one estimate was obtained using the insect's measured mass, and one using mass as estimated from length using allometric equations. The latter estimates were made because the length of the insect is frequently easier to measure than the mass.

Validation. All four estimates of H_{dir} were obtained using data from the half of the insects for which A_H had been obtained. They were validated by using each to predict the temperature responses of the nymphs which had not been used to obtain the estimates. Precision and accuracy of the predictions were assessed using regressions of the observed value of CHANGE on the value predicted using H_{dir} and $\hat{A}_s$.

Simulations

Results of the preceding analyses were exploited to learn how equilibrium body temperature elevation responds to variation in insect size, insect orientation, direct solar radiation and wind speed. Equilibrium temperature elevation was determined using equation (2), omitting the term describing the effect of diffuse solar radiation, by setting $\partial \Delta T / \partial t = 0$, and solving for ΔT. To facilitate comparison and contrast with published results, direct solar energy was expressed in two ways: as insolation (W·m⁻²) and as energy intercepted by the insect (W). For the simulations, total incoming solar energy was set at 800 W·m⁻², and the zenith angle at 45°. The direct component of this energy was estimated using the algorithm described by Spitters *et al.* (1986), which incorporates the effects of solar zenith angle and the ratio of measured radiation to the theoretical maximum value at the top of the atmosphere (*c.* 1300 W·m⁻²). By this method, estimated direct solar radiation was 441.2 W·m⁻².

In the simulations, insect mass was varied from 0.03 to 0.30 g and wind from 0 to 5 m·s⁻¹. Simulations were performed for insects oriented in a variety of orientations to the solar vector.

Results and Discussion

The experiment was conducted from 30 June to 20 July 1994, and consisted of fourteen trials, with three or four insects per trial. In total, forty-nine insects were used; masses ranged from 0.0188 to 0.2965 g, and lengths from 8.0 to 22.0 mm. The visible-spectrum absorbance of the nymphs was normally distributed with a mean of 0.722 and a standard deviation of 0.045.

Each trial consisted of from sixteen to twenty-one runs in which the combinations of orientation and shade level differed. Approximately ten 12 s means were collected in each run. Unshaded total solar radiation ranged from 760 to 1014 W·m⁻²; the lowest solar radiation under shade was 90 W·m⁻².

The mass and the four physical measurements of each insect were strongly interrelated (Table 1). Each of the physical measurements can be estimated from mass with $r^2 > 0.81$; mass and the remaining physical measurements can be estimated from length with slightly less precision.

Silhouette area estimates were strongly related. Where measurements are in mm², $A_p = 5.38 + 0.96 \cdot \hat{A}_p$ ($F = 818.3$; df = 1, 211; $P(>F) \le 0.0001$; $r^2 = 0.79$). The standard errors of the intercept and slope estimates were 2.18 and 0.033, respectively. Both slope and intercept are significantly > 0 ($P(>t) \le 0.0001$). The significant intercept probably occurs because the representation of the insect as a trapezoidal prism neglects the contribution of

Table 1. Parameter estimates from logarithmic regressions comparing insect dimensions to length or mass.

	Model $\ln(Y) = \ln(\alpha) + \beta \cdot \ln(\text{mass})$					
Insect dimension (Y)[a]	$\ln(\alpha)$		β			
	Est	SE	Est	SE	F	r^2
A	1.6489	0.0427	0.2623	0.0171	243.5	0.8100
B	2.0087	0.0376	0.2581	0.0151	293.1	0.8420
C	2.1016	0.0468	0.3055	0.0188	264.3	0.8277
D	3.5510	0.0304	0.3909	0.0122	1023.8	0.9490
(A+C)/2	1.9034	0.0301	0.2881	0.0121	569.4	0.9119
	Model $\ln(Y) = \alpha + \beta \cdot \ln(\text{length})$					
A	−0.6733	0.1168	0.6479	0.0446	214.3	0.7957
B	−0.2858	0.1008	0.6412	0.0382	281.7	0.8367
C	−0.5934	0.1314	0.7509	0.0498	227.2	0.8051
(A+C)/2	−0.6406	0.0891	0.7090	0.0338	440.8	0.8891
mass	−8.7426	0.2002	2.4278	0.0759	1023.8	0.9490

In all regressions, df = 1, 47 and $P(>F) \le 0.0001$. Est, estimate; SE, standard error.

[a] A, dorsal breadth; B, depth; C, ventral breadth; D, length. Dimensions in millimetres. Mass in grams.

appendages to the shadow cast. Nonetheless, using this regression equation for a sample of insects, A_p from image analysis can be estimated with *c.* 80% precision from $\hat{A}_p$.

Statisical analyses

The analysis of variance model which quantified the effects of the experimental variables on body temperature elevation was highly significant ($F = 11.64$, $dfe = 75{,}229$; $P(>F) \leq 0.0001$; $r^2 = 0.79$). The effect of direct solar radiation (QDIR/[$M \cdot c_p$]) on temperature change was highly significant ($P(>F) \leq 0.0001$), but the effect of diffuse solar radiation (QDIF/[$M \cdot C_p$]) was not significant ($P(>F) = 0.5494$). Trial, insect nested within trial, and axis of rotation were not significant, either as main effects or within interactions (all $P(>F) > 0.1$). The absorbance of the insect was not significant as a main effect, but there was a significant interaction between absorbance and trial ($P(<F) = 0.0232$); this simply means that the absorbance of the insects varied irregularly among trials and does not imply a meaningful physical effect. Therefore in subsequent analyses the effects of trial, insect nested within trial, absorbance, and QDIF/[$M \cdot c_p$] were subsumed into the error term.

Diffuse solar radiation had no significant effect on the heating rate of grasshopper nymphs. One possible explanation of this result is that the allometric equation used to estimate grasshopper surface areas may have been imprecise. However, in the study in which this relationship was derived (Lactin & Johnson, 1997), the correlation coefficient (r^2) was >0.95; although application of the equation to the different insects used in the present study may have resulted in some error, it seems very unlikely that the surface area estimate could be so imprecise as to reduce any significant effect to $P(\text{QDIF} = 0) > 0.5$.

Table 2. Regressions of change in body temperature elevation (°C·s^{-1}, after adjusting for temperature change by convection and greybody reradiation), on (energy intercepted)/(c_p·insect size). Energy intercepted was estimated in two ways, and size in two ways; see text for details.

Silhouette estimate	Intercept (°C·s^{-1}) Est	Intercept (°C·s^{-1}) SE	Slope (dimensionless) Est	Slope (dimensionless) SE	*F*	r^2
	Size represented by mass					
A_p[a]	–0.0025	0.0089	0.688	0.097	170.3	0.6531
$\hat{A}_p$[b]	–0.0013	0.0904	0.662	0.096	159.8	0.6368
	Size represented by a function of length					
A_p	0.0087	0.032	0.602	0.090	154.3	0.6304
$\hat{A}_p$	0.0054	0.032	0.609	0.088	160.9	0.6401

In all regressions, df for the *F*-test = 1, 27 and slopes are highly significant ($P(>|t| < 0.0001$). Standard errors and statistical tests are based on the number of insects used. Est, estimate; SE, standard error.

[a] Area of silhouette on plane perpendicular to solar vector, measured using image analysis.

[b] Area of silhouette on plane perpendicular to solar vector, estimated using approximating the insect as a trapezoidal prism.

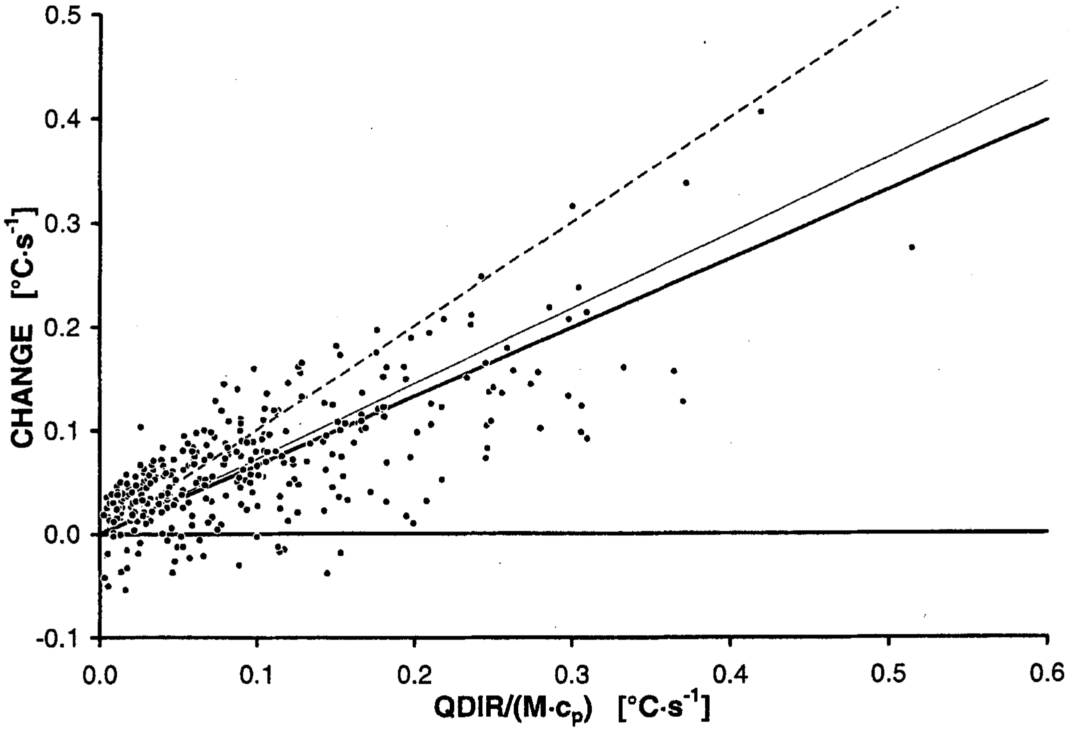

Fig. 1. Rate of change in body temperature, corrected for temperature loss by convection and greybody reradiation (CHANGE, °C·s^{-1}), versus energy intercepted per unit heat capacity (QDIR/[M·c_p]), with regression line. Energy intercepted was estimated using silhouette area from image analysis; mass measured. Heavy solid line: best-fit linear regression of observed rate. Broken line: observed rate = maximum possible rate. Light solid line: rate expected if H_{dir} = measured visible-spectrum absorbance (0.722).

The solar heating coefficient

Estimation. The regressions of CHANGE on all four estimates of QDIR/[$M{\cdot}c_p$] were highly significant (Table 2). Fig. 1 illustrates the relationship between CHANGE and QDIR/[$M{\cdot}c_p$], using measured mass and QDIR calculated using A_s; regressions using QDIR/[$M{\cdot}c_p$] obtained by the other methods were similar. The intercepts were not significant ($P(>|t|) > 0.5$), whether N_{ins} or N_{obs} was used as the error term. The spinning-cup anemometer has a stall speed of $0.447\,m{\cdot}s^{-1}$ and a reading scale quantized in units of $1.6\,m{\cdot}s^{-1}$. This limited resolution certainly contributed to the variation observed in Fig. 1.

All four estimates of H_{dir} (i.e. regression slopes) were significantly greater than 0 ($P(>F) < 0.01$), and were similar. The estimates ranged from 0.690 (SE = 0.098) to 0.603 (SE = 0.087). The largest estimate was only 1.14 times the smallest, and none differed significantly from any other (pairwise t-tests, $P(>|t|) > 0.05$). These results indicate even when the procedures are simplified by applying allometric relationships and geometric approximations to estimate mass, silhouette area and energy intercepted, the resulting estimates of H_{dir} are acceptably close to the values obtained by measuring these values in detail.

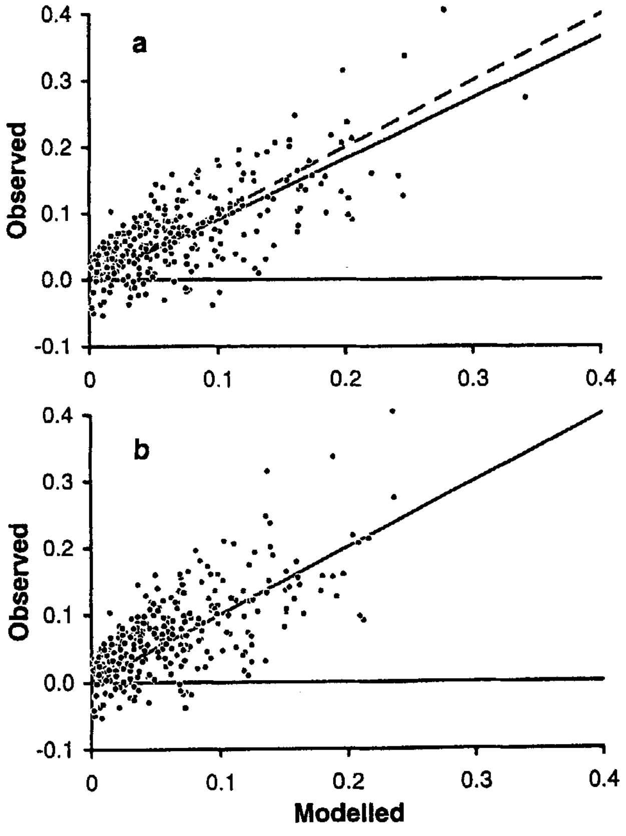

Fig. 2. Validation of algorithm predicting rate of body temperature change [$°C{\cdot}s^{-1}$] due to heating by direct solar radiation [$W{\cdot}g^{-1}$]. (a) Modelled rate obtained using mass to represent insect size. (b) Modelled rate obtained using length to represent insect size. Solid oblique line, best-fit regression (forced through 0, 0); this line does not differ significantly from 1:1 agreement (broken oblique line, obscured in panel b).

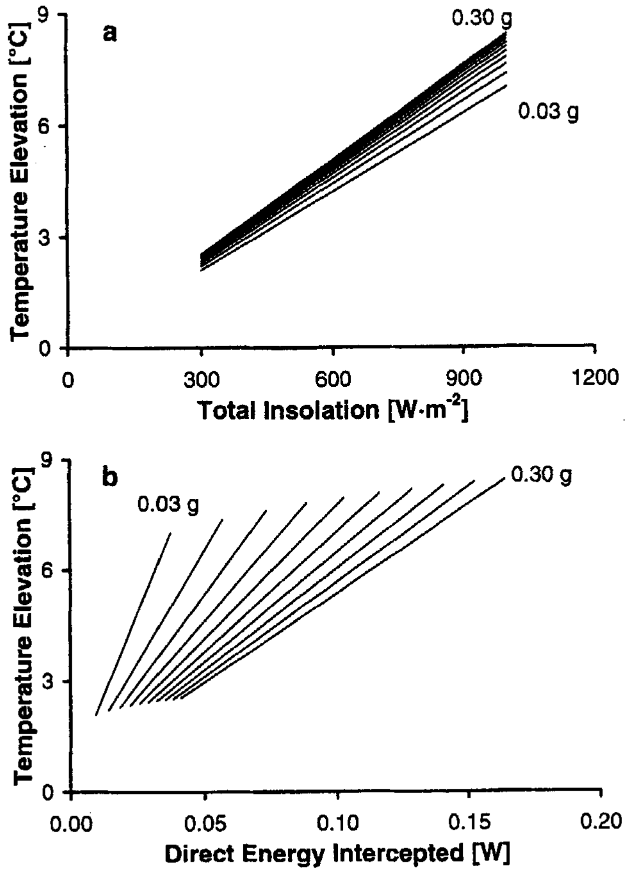

Fig. 3. Simulated equilibrium body temperatures for insects of mass 0.03–0.30 g, in increments of 0.03 g, at insolation from 300 to $1000\,W{\cdot}m^{-2}$. All insects broadside to solar vector. Wind speed = 0. In both figures, line segments join results at 300 and $1000\,W{\cdot}m^{-2}$. (a) Temperature elevation versus insolation. At a given insolation, temperature elevation increases with body mass. (b) Temperature elevation versus energy intercepted. At a given level of energy intercepted, temperature elevation *decreases* with body mass.

The value of H_{dir} is the observed rate of temperature change, as a proportion of the maximum possible rate. The latter rate could occur only if all incident direct energy were absorbed and therefore, H_{dir} must be similar to the proportion of incident energy absorbed. In Fig. 1 a broken line is included which represents the maximum rate; the observed rate (heavy solid line) is significantly less than this. If the measured visible-spectrum absorbance (i.e. 0.722) pertains to the entire spectrum, and if all energy not reflected is absorbed, the rate of temperature change would correspond to the fine solid line. Although all measured slopes were slightly less than 0.722, none was significantly different from this value (pairwise t-tests, all $P(>|t|) > 0.3$). Clearly, the observed temperature responses are very similar to those expected if visible-spectrum absorbance is the same as full-spectrum absorbance. This observation indicates that the former may be an adequate substitute for H_{dir}.

This conclusion suggests strongly that the visible-spectrum absorbance of the nymphs greatly influences temperature elevation, yet the ANOVA did not detect any statistically-significant effect of absorbance. One explanation for this discrepancy is that the range of variation in absorbance among our nymphs may have been too small, compared to random variation in temperature elevation, to reveal any correlation.

Validation. For the twenty-seven insects not used to estimate H_{dir}, regressions of observed CHANGE on CHANGE as predicted using H_{dir} estimates were highly significant and demonstrated good agreement (Fig. 2). Regression intercepts were not significant ($P(>F) > 0.2$), so lines were forced through the origin. Using measured insect mass the resulting regression had slope = 0.910 (SE = 0.0960); $F = 90.0$; $dfe = 1, 25$; and $r^2 = 0.7692$. Where insect mass was estimated from length, the regression had slope = 1.004 (SE = 0.114); $F = 78.0$; $dfe = 1, 25$; and $r^2 = 0.7423$. Standard errors and statistical tests were based on the N_{ins} (i.e. 27). In both cases, the slope was significantly greater than 0 but not significantly different from 1 ($P(>|t|) > 0.50$). Therefore the predicted values of CHANGE do not differ significantly from observed values, and estimates of H_{dir} may be applied validly to insects other than those on which they were derived.

Simulations

When energy influx was expressed as insolation ($W \cdot m^{-2}$), equilibrium body temperature elevation increased with body mass (Fig. 3a) and length. This result is consistent with published reports in which temperature elevation of individual insects increases linearly with increasing insolation at a rate of 0.004 to 0.03°C/($W \cdot m^{-2}$), with the rate increasing with insect body mass (e.g. Pepper & Hastings, 1952; Digby; 1955; Henson, 1958; Stower & Griffiths, 1966; Edney, 1971; Cena & Clark, 1972; Lactin & Holliday, 1994). Our simulations result in equilibrium body temperature elevations of *c.* 0.008°C/($W \cdot m^{-2}$), which agrees well with these published values. However, expressing energy influx in this way obscures the underlying physical mechanism by which body temperature is determined.

When energy influx was expressed as energy intercepted (*W*), the results were very different. Algebraic solution of equation (2), omitting the effects of diffuse solar radiation, demonstrates that at a specified amount of energy intercepted, equilibrium body temperature elevation changes as the inverse of some exponent of mass, i.e. this quantity *decreases* with increasing insect size. Fig. 3(b) illustrates that at a specified amount of energy intercepted, small insects attain a greater equilibrium body temperature elevation than do larger ones, and that this elevation increases faster with energy intercepted in small insects than it does in larger ones. Both of these effects occur because a given amount of energy heats less tissue in a small insect than in a large one. The increase in equilibrium body temperature elevation with size that is observed when energy influx is expressed as insolation ($W \cdot m^{-2}$) occurs because the amount of energy intercepted at a given insolation increases with insect size. Therefore, the range of heating coefficients observed when energy is expressed as $W \cdot m^{-2}$ is a consequence of the choice of units.

Other simulations (not presented) revealed the consequences of reorientation in various axes, on body temperature elevation. Changing pitch or yaw angles changed the amount of energy the insects intercepted by a factor of 4, whereas the maximum effect of change in roll orientation on energy intercepted was less than 1.12. These results suggest that in *M.sanguinipes*, and similarly shaped acridids, change in the roll angle would be a less effective thermoregulatory tactic than are changes in pitch or yaw.

Simulations also revealed how insect size and wind speed combine to affect equilibrium body temperature elevation (Fig. 4). At a yaw angle of 90° (Fig. 4a) the insects temperature elevation was 2–3 times greater than at 0° (Fig. 4b); this difference is slightly less than the 4-fold difference in amount of energy intercepted because of the increasing influences of convective and reradiative temperature loss with increasing body temperature elevation. At a yaw angle of 0°, modelled equilibrium body temperature elevation was relatively independent of mass; closer examination of the simulation output (data not presented) revealed

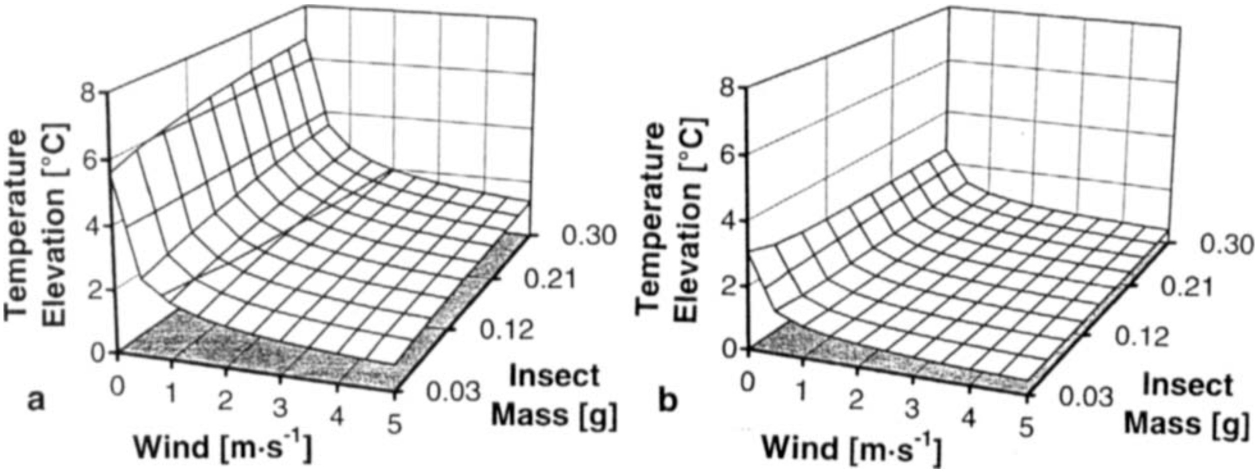

Fig. 4. Equilibrium body temperature elevation of *M.sanguinipes* nymphs of a range of masses and wind speeds, calculated using equation (2). Total solar radiation = 800 $W \cdot m^{-2}$; Direct solar radiation = 441.2 $W \cdot m^{-2}$; Zenith angle = 45°. (a) Insects perpendicular to solar vector. (b) Insects facing solar vector.

that this effect occurred because of the effects of the intercept (probably due to the contributions of appendages to the shadow) in the regression of A_p on $\hat{A}_p$.

The equilibrium body temperature elevations calculated in this study are slightly higher than those reported reported in *Melanoplus packardii* nymphs (Lactin & Johnson, 1996b), although comparison is qualitative because in that study temperature elevation was expressed as a function of total solar radiation, whereas in the present study it was expressed as a function of direct solar radiation. Nonetheless, both studies demonstrate that equilibrium body temperature elevation decreases with mass at a given amount of energy intercepted, but that this elevation increases with mass at a given solar radiation. This similarity in results confirms the validity of this method of estimating equilibrium body temperatures from the component biophysical functions. Further, it suggests that the simulation model described here may be applied to species of grasshoppers which are similar in size and shape to *Melanoplus sanguinipes*, substituting measured visible-spectrum absorbance for H_{dir}, if necessary.

Separating the effects of the various factors which affect equilibrium body temperature elevation has several distinct advantages over the method of relating this elevation empirically to solar radiation ($W \cdot m^{-2}$). Equilibrium body temperature elevation can be estimated at any combination of solar radiation and wind speed for grasshopper nymphs of any size and orientation. By specifying insect dimensions and expressing energy as *W* intercepted, and applying the appropriate equations, the effects of wind speed and orientation to the sun can be examined simultaneously. By separating the effects of these factors, the results of varying them emerge as a consequence of physical laws. The physical fundamentality of the approach means that probably it can be adapted to apply to any small ectotherm. In theory, the historical approach of representing energy influx as $W \cdot m^{-2}$ could be used to estimate the combined effects of changing solar radiation, orientation and wind on insects of difference size, but would require a greater number of empirical relationships than the method demonstrated here. Furthermore, this approach would not illuminate the underlying biophysical similarity of the temperature response.

Body temperature can be estimated if air temperature is known at the location occupied by the insect. Improved understanding of the mechanisms by which insects control their body temperature, and the limits to this control, will benefit numerous fields including ecology, biogeography and economic entomology.

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