Effects of Insolation and Body Orientation on Internal Thoracic Temperature of Nymphal *Melanoplus packardii* (Orthoptera: Acrididae)

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ABSTRACT The effect of insolation on body temperature of nymphal Packard grasshoppers, *Melanoplus packardii* Scudder, was measured in the field. Live nymphs were each restrained in a series of orientations to the sun, and insolation was adjusted using a shade cloth. Internal thoracic temperature was allowed to stabilize and was compared with that of a reference nymph restrained in a sunshade. Equilibrium body temperatures of insolated nymphs exceeded that of the reference nymph by an amount (ΔT_b) which increased with energy intercepted (*ENERGY*) and insect size (*SIZE*) by a relationship of the form $\Delta T_b = a \cdot ENERGY \cdot SIZE^b$. When insect size was expressed as mass (grams), the estimates of a and b were 18.76 and -0.312, respectively ($r^2 = 0.6198$); when insect size was expressed as length (millimeters), a and b were 826.66 and -1.133, respectively ($r^2 = 0.6463$) These results allow estimation of equilibrium body temperature elevation of *M. packardii* nymphs from solar radiation, the zenith angle of the sun, insect size, and the orientation of the insect to the sun.

KEY WORDS grasshopper, body temperature, thermoregulation, size effects, biophysics

MANY TERRESTRIAL ECTOTHERMS can control their body temperature (T_b) by exploiting environmental heterogeneity (Huey and Slatkin 1976, May 1979). Usually, T_b exceeds air temperature (T_a) and tends to be near the optimum for 1 or more ecologically important temperature-dependent physiological processes (Heinrich 1977, Huey and Kingsolver 1989).

In diurnal ectotherms of mass <1 g, solar radiation (insolation) is the most important source of heat gain (Stevenson 1985). In insects, maximum equilibrium T_b elevation (i.e., $T_b - T_a$) increases linearly with radiation intensity, and with the mass of the insect (Pepper and Hastings 1952, Digby 1955, Henson 1958, Stower and Griffiths 1966, Edney 1971, Cena and Clark 1972). Many insects have taxic or kinetic responses that affect the amount of radiation intercepted (May 1979, Heath and Wilkin 1970); they may thereby exercise considerable control over T_b (May 1982, Kemp 1986, Carruthers et al. 1992). Therefore, in ectothermic insects, energy interception is determined by insolation intensity and the area presented to the insolation source. We were interested in quantifying these effects separately, to allow simulation of the observed response from the component effects.

This study was conducted on field-collected nymphal Packard grasshoppers, *Melanoplus packardii* Scudder. The purposes were to quantify the effects of insolation intensity on equilibrium T_b elevation; orientation to the sun on T_b elevation; and

insect size on the relationship between energy interception and equilibrium T_b elevation.

Materials and Methods

Live *M. packardii* nymphs were restrained in known orientations to the sun, and equilibrium T_b elevation was compared with the amount of solar energy intercepted. Insect orientation was manipulated using an experimental device which consisted of 2 wooden boards (60 by 15 by 1.5 cm), mounted one atop the other with the long axes connected by hinges. Six pivots were mounted perpendicular to the upper board, and one size 14 cork stopper (≈3.2 cm maximum diameter) was mounted on each with the pivot inserted into a bored hole in the center of the base of the cork.

The device was placed in a mowed grass area, leveled ≈10 cm above the ground, and aligned with its long axis perpendicular to the sun vector and the hinged side away from the sun. The upper board was adjusted to match the elevation angle of the sun. The orientations of the long axis and the upper board were adjusted about every 15 min during the experiments.

Each experimental grasshopper nymph was restrained by adhering a piece of cork (2 by 2 by 3 mm) to its thoracic sternites using upholstery adhesive (EC2218, 3M, London, ON). The hind legs of each insect were immobilized by gluing them to the abdomen with the same adhesive. The cork

piece was then attached by an insect pin to 1 of the large stoppers on the experimental device. One nymph was mounted on each stopper. The insects were ≈5 cm above the upper board.

Orientation of the insects to the sun was adjusted by rotating the large corks on the pivots, aligning the insects with calibration marks on the experimental device. Orientation was varied independently around 1 of 3 mutually perpendicular axes, which were defined relative to the grasshopper. The x-axis passed from the head to the tip of the abdomen, the y-axis from side to side, and the z-axis from dorsum to venter. Rotations about the x-, y-, and z-axes were termed roll, pitch, and yaw, respectively.

Insect orientation was varied with respect to the solar vector (i.e., a line joining the insect and the sun), in increments of 30°. Yaw angles were from 0° (x-axis parallel to the solar vector, with the frons toward the sun) to 90° (x-axis perpendicular to the solar vector, with the left side toward the sun). Roll angles were from 0° (x-axis perpendicular to the solar vector, with the dorsum toward the sun) to 90° (x-axis perpendicular to the solar vector, left side toward the sun). Pitch angles were from 0° (x-axis parallel to the solar vector, with the frons toward the sun), through 90° (x-axis perpendicular to the solar vector, with the dorsum toward the sun) to 180°.

Grasshopper T_b was measured using 0.127-mm-diameter copper-constantan, teflon-insulated thermocouples (Omega, Stanford, CT) inserted to a depth of ≈2 mm through an incision between the prothorax and mesothorax on the right side. This side of the insect was not exposed to direct sunlight during the experiment.

The T_b of insolated grasshoppers was compared with that of a similarly restrained reference grasshopper in a sunshade. The temperature of this grasshopper is considered to be T_a. A grasshopper was used to provide the reference temperature because the temperature of a bare thermocouple changed too quickly to provide a reliable basis for comparison.

The sunshade was constructed of 4 parallel aluminum plates (1 mm thick), which were painted flat black on one side and flat white on the other. The inner pair of plates measured 10 by 10 cm and were separated by 1.5 cm. The outer pair of plates measured 12 by 12 cm; the separation between inner and outer plates was 1 cm. The top 2 plates were mounted with the black side down and the others with black side up. The sunshade was mounted within 0.3 m of the experimental device, with the plates horizontal; it was set at the same height and shaded in the same manner as the restrained insects. The reference grasshopper, which was restrained in the same manner as the experimental nymphs, was pinned to a foam cylinder (4 cm long by 2 cm diameter) inserted between the inner plates. The insect did not touch the plates. To minimize forced convection we chose an ex-

perimental site that was sheltered from the wind, and conducted the experiment only on calm days.

Insolation was measured using a pyranometer (LI-200SZ, LI-COR, Lincoln, NE). Insolation intensity was manipulated using 42-cm^{-2} mesh black nylon screen mounted on a wooden frame (1 by 1 m) placed perpendicular to the solar vector, between the nymphs and the sun, 1 m from the nymphs. The shade treatments were 0, 1, 2, or 4 layers of cloth.

In each trial, each of 6 grasshoppers was presented in from 2 to 7 orientations (mode = 4) under each of the 4 shade treatments. Insolation, T_a and T_b were measured every 0.5 s; these measurements were averaged and recorded every 12 s using a data logger (model 21X, Campbell, Edmonton, AB). Measurements were taken for at least 3 min, or until $T_b - T_a$ appeared to have stabilized, as judged by comparing readouts on the data logger. The stabilized value was used as the estimate of equilibrium T_b elevation, and was compared with the contemporaneous insolation measure. Before analysis, time–temperature trends were plotted, and T_b elevation had failed to stabilize in only 1 run in 1 trial; this case was deleted.

On completion of each trial, 4 physical measurements were taken from each insect: length from the frons to the tip of the abdomen; depth from the dorsum to the venter; dorsal breadth across the mesonotum; and ventral breadth across the widest part of the sternum, including the width of the metafemora. Dimensions were measured to 0.5 mm using hand-held calipers. The insects were then classified by instar, weighed (grams of fresh body mass), and stored individually at −40°C.

For analysis, solar energy intercepted by each grasshopper (in watts, W) was estimated as the product of the pyranometer reading (W · m^{-2}) and the area of the insect's shadow on a horizontal surface (A_s), in square meters. Shadow area was used because the pyranometer measures insolation incident on a horizontal surface. This estimate was made by measuring the shadow area (A_p) of the insect on a plane perpendicular to the solar vector, then converting this to A_s using the relationship $A_s = A_p/\cos(Z)$, where Z is the zenith angle of the sun, as calculated from Julian date, solar time and site latitude (Robertson and Russelo 1968).

The value A_p was measured using image analysis. The nymphs were mounted under a Dage 68 black and white video camera (DAGE-MTI, Michigan City, IN), and were presented in the same angles and orientations relative to the line from lens to object, as had they been presented relative to the solar vector in the field trials. Images were acquired at standard magnification, input to an image analyser (Tracor Northern 8502; Noran, Middleton, WI), and converted to digital images (512 by 512 pixel) with a greyscale range of from 0 (perfect reflectance) to 256. Two greyscale thresholds were adjusted to isolate the image of the grasshopper from the background, and the number of pixels

comprising the image was converted to A_p using an empirically derived calibration constant.

Preliminary analyses indicated that T_b elevation (ΔT_b) was described by a function of the form

$$\Delta T_b = a \cdot ENERGY \cdot SIZE^b \qquad (1)$$

where *ENERGY* is solar energy intercepted, *SIZE* is either the mass or the length of the insect, and $b < 0$. The following conclusions were unaffected by mean reflectance of the insects, as calculated from the image analyser greyscale reading, probably because the value was similar ($\approx 40\%$) in all insects.

Parameters a and b in equation 1 were estimated using iterative nonlinear regression (PROC NLIN, Marquardt algorithm, SAS Institute 1989), representing size by either insect mass (in grams) or insect length (in millimeters). To reduce variation sufficently to allow the regressions to converge, values of *ENERGY* were rounded to classes of 0.005 W, insect mass to classes of 0.01 g, and insect length to classes of 0.5 mm, and parameters were estimated using the class means, weighted by the number of observations in each class.

In PROC NLIN, all observations are treated as independent, and the standard errors of the estimates are calculated using the number of class means (N_{obs}, varying by analysis). However, the observations actually are repeated measures on insects, and so the standard errors should be based on the number of true replicates, i.e., the number of insects (N_{ins}). Therefore, all standard errors output by PROC NLIN were adjusted to reflect the number of insects by multiplying by $(N_{obs}/N_{ins})^{1/2}$. Similarly, model F values were calculated using N_{ins} as the degrees of freedom for the denominator.

Analysis of covariance (ANCOVA, PROC GLM, SAS Institute 1989) was then used to quantify the effects of other experimental factors on the relationship between T_b elevation and $ENERGY \cdot SIZE^b$. Additional factors tested were trial, insect nested within trial (insect [trial]), and axis of rotation; all 2-way interactions were also tested. Imbalance in the distribution of instars among trials, which resulted from natural population phenology of the insects, disallowed direct comparison of the effects of instar on the response. Inspection of plots suggested that any instar effects were related to size differences.

Equation 1 reveals that at a given amount of energy intercepted, a small insect will attain a greater T_b elevation than a large insect. However, this interpretation is incomplete, because at a given level of insolation (W · m^{-2}), a small insect intercepts less energy than a large one. This effect complicates interpretation of the results. Furthermore, T_b elevation has been typically expressed as a function of insolation [W · m^{-2}] (e.g., Pepper and Hastings 1952, Digby 1955, Henson 1958, Stower and Griffiths 1966, Edney 1971, Cena and Clark 1972), and equation 1 is not easily comparable with these reports. Therefore, we undertook a series of

simulations to provide more complete understanding of the effects of insect size, insolation, the zenith angle of the sun, and the orientation of the insect to the sun on T_b elevation, and to allow comparison to published reports. The procedure was as follows.

To allow simulation of a range of insect sizes, regression analysis was used to quantify the relationships of insect depth, dorsal breadth, ventral breadth, and mass to insect length. The size of the simulated insect was specified using either length or mass, and these regression relationships were used to obtain the other measurements.

A 2nd estimate of shadow area on a horizontal surface ($\hat{A}_s$) was obtained geometrically, representing each grasshopper as the trapezoidal prism defined by the length, depth, dorsal breadth, and ventral breadth measurements. Contributions of sides and faces to the area of a shadow on a surface perpendicular to the solar vector, were determined by applying trigonometric functions to the angle of the insect relative to the solar vector, and $\hat{A}_s$ was obtained by dividing this by the cosine of the simulated solar zenith angle.

Temperature elevation was simulated under a range of insolations (0–1,200 W · m^{-2}) for insects with masses from 0.05 to 0.50 g or lengths from 11.5 to 24.5 mm; the extremes of length and mass approximately correspond. Simulated T_b elevation was compared with insolation level (W · m^{-2}) and to the amount of energy intercepted by the insect (watts).

Results and Discussion

The experiment was conducted from 12 July to 6 August 1993 inclusive, in 10 trials involving 20 fourth-instar and 33 fifth-instar grasshoppers. A total of 612 data points was collected.

For each insect, the relationship between temperature elevation and insect size was linear, but as insect size increased, the slope and intercept of this regression decreased and increased, respectively (Fig. 1). These results indicate that the individual linear regressions are merely local approximations of a general nonlinear trend.

Equation 1 was fitted successfully to the data, whether insect size was expressed as mass or length. Parameter estimates are given in Table 1. Although there is clearly considerable variation in the observed trends, the fitted curves have $r^2 > 0.6$. Where insect size was expressed as length, the standard errors of the estimates, as a proportion of the estimates, were much greater than where insect size was expressed as mass. This comparison suggests that mass is the most appropriate physical factor to be used, because it is a direct measure of the amount of tissue to be heated. Length is simply a proxy for mass, and the correlation between length and mass is imperfect. Despite this inflation of standard error estimates, comparison of F and r^2 statistics indicates that the model in which size
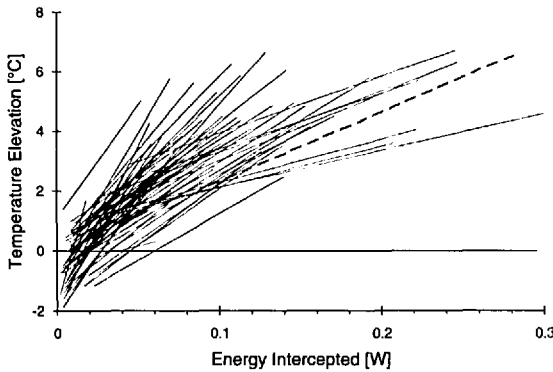
Fig. 1. Equilibrium body temperature elevation on energy intercepted for each insect. Each fine line segment represents a linear regression over the range of values of the energy measure to which the insect was exposed. The heavy broken lines represent simulation predictions for insects of mass 0.05 (left) and 0.50 g.

was represented by length described the data slightly better than that in which size was represented by mass. Thus length is an adequate measure of size, and may be easier to use than mass.

The ANCOVA models testing the effects experimental factors on the relationship between ΔT_b and $ENERGY \cdot SIZE^b$ were highly significant, whether insect size was expressed as mass or length (Table 2). In both cases, $F = 14.9$; df = 127, 484; $P \le 0.0001$; $r^2 = 0.7962$. These overall model statistics are the same because the ANCOVA was performed on transformations of the same data; differences occur only in the partitioning of variance among model components. Axis of rotation had no effect on the relationship between ΔT_b and $ENERGY \cdot SIZE^b$, either alone or as an interaction ($P > 0.7$). This result indicates that no orientation is better than any other at absorbing energy or converting it to heat, and that the relationship between T_b elevation and energy intercepted is caused entirely by the change in the amount of energy intercepted.

Regression intercepts differed among trials (significant trial effect), but the regressions did not differ among insects within trials (no significant effect of insect[trial] either alone or as an interaction

with $ENERGY \cdot SIZE^b$). We attribute these results to our measurement of T_b elevation relative to a baseline established using another insect. Apparently, differences in thermal equilibrium among individuals resulted in a distribution of baselines for comparison, which translated to differences in intercept among trials but did not affect intercepts or slopes within trials.

The trial $\times$ $ENERGY \cdot SIZE^b$ interaction was significant for both measures of insect size. This result indicates that the slope of the regression of ΔT_b on $ENERGY \cdot SIZE^b$ differed among trials. Several factors could explain this observation. First, we used the final T_b measure as the estimate of equilibrium T_b; the correlation between these quantities was probably imperfect. Second, we used the contemporaneous insolation reading as the measure of the value to which T_b elevation had responded; this is also an imperfect approximation because insolation often varied over time, and there was a time lag in the resulting change in T_b. Third, the temperature of the irradiated and shaded sides of the thorax of *M. sanguinipes*, which is similar in size and shape to *M. packardii*, can differ by as much as 2.5°C (Pepper and Hastings 1952); despite our attempts to standardize thermocouple insertion depth, this internal temperature gradient probably contributed to the range of slope estimates. Finally, conditions varied slightly among trials, and slight differences in unmeasured meteorological factors, e.g., diffuse radiation, may have affected the relationship of T_b elevation to $ENERGY \cdot SIZE^b$. Despite these sources of error, it was possible to quantify the relationship above the statistical noise.

Strong relationships were detected among the measurements taken of each insect. The insect dorsal breadth, ventral breadth, and depth were each proportional to length; proportions (estimate $\pm$ SE) were 0.204 ± 0.003, 0.279 ± 0.003, and 0.305 ± 0.004, respectively. In all cases, $F > 5,000$; df = 1, 81; $P \le 0.0001$; and $r^2 > 0.98$. Mass (in grams) was related to length (in millimeters) by equation 2:

$$\ln(\text{mass}) = c + d \cdot \ln(\text{length}), \qquad (2)$$

where $c = -10.87 \pm 0.489$ ($\pm$SE) and $d = 3.174$

Table 1. Parameter estimates for $\Delta T_b = a \cdot ENERGY \cdot SIZE^b$ (equation 1 in text) relating body temperature elevation to energy intercepted, using 2 size measures

| Size measure | Parameter estimates | | | | | | F | r^2 |
| | a | | | b | | | | |
	Est	SE(1)[a]	SE(2)[b]	Est	SE(1)	SE(2)		
Mass	18.76	1.57	4.05	−0.312	0.048	0.124	91.3	0.6198
Length	826.66	362.83	935.44	−1.133	0.153	0.394	101.2	0.6463

For both equations, $P < 0.0001$; df = 2, 50. Est, estimate; SE, standard error.
[a] Value output by PROC NLIN (i.e., calculated using number of observations).
[b] Value corrected to represent number of true replicates (i.e., number of insects).

Table 2. Results of ANCOVA testing relationship of body temperature elevation to experimental factors

Variance source	Mean square	df	F	P
Size measured by mass				
ENERGY · MASS $^{0.312}$	246.093	1	27.64[a]	≤0.0001
Trial	11.583	10	14.41[b]	≤0.0001
Trial × ENERGY · MASS $^{-0.312}$	8.903	10	7.59[c]	≤0.0001
Insect(trial)	0.804	52	0.84[d]	0.7752
Insect(trial) × ENERGY · MASS $^{-0.312}$	1.173	52	1.13[d]	0.1398
Axis[e]	0.110	1	0.12[d]	0.7344
Axis × ENERGY · MASS $^{0.312}$	0.013	1	0.00[d]	0.9076
Size measured by length				
ENERGY · LENGTH $^{-1.133}$	234.380	1	27.59[a]	≤0.0001
Trial	11.716	10	14.56[b]	≤0.0001
Trial × ENERGY · LENGTH $^{-1.133}$	8.494	10	8.76[c]	≤0.0001
Insect(trial)	0.804	52	0.84[d]	0.7741
Insect(trial) × ENERGY · LENGTH $^{-1.133}$	0.970	52	1.02[d]	0.4467
Axis	0.001	1	0.00[d]	0.9705
Axis × ENERGY · LENGTH $^{-1.133}$	0.071	1	0.07[d]	0.7850

For both analyses, $F = 14.9$; df = 127, 484; $P \leq 0.0001$; and $r^2 = 0.7962$.
[a] Error term: trial × ENERGY · SIZE[b].
[b] Error term: insect (trial).
[c] Error term: insect(trial) × ENERGY · SIZE[b].
[d] Error term: model residual.
[e] Axis in which insect was rotated.

± 0.174. This regression had $F = 332.7$; df = 1, 81; $P \leq 0.0001$; and $r^2 = 0.8062$.

By regression analysis, the geometrically obtained estimate of the shadow cast by the grasshopper on a horizontal surface $(\hat{A}_s)$ was strongly correlated with the value obtained by image analysis (A_s). Where areas were expressed in square millimeters,
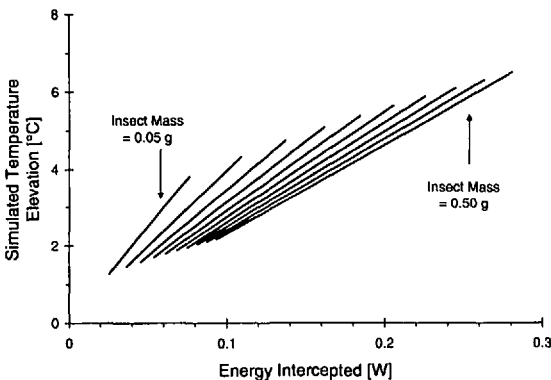
$$A_s = 15.0 + 0.994 \cdot \hat{A}_s. \quad (3)$$

This regression has $F = 7,687.5$; df = 1, 565; $P \leq 0.0001$; and $r^2 = 0.9128$. The standard errors of

Fig. 2. Simulated equilibrium body temperature elevation of *M. packardii* nymphs as a function of insect size and energy intercepted. Insects were assumed to be oriented perpendicular to the solar vector; solar zenith angle = 45°; insolation = 300–1,200 W · m^{-2}. Each line segment represents the limits to body temperature elevation for one insect. From left to right, insect mass increases from 0.05 to 0.50 g in increments of 0.05 g.
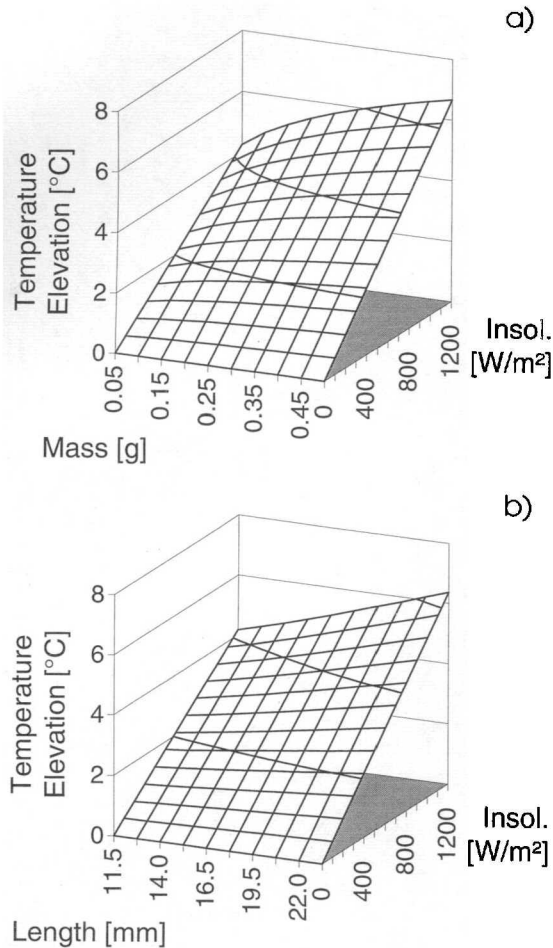
the intercept and slope were 0.12 and 0.0095, respectively. The intercept is significantly >0, probably because the geometric representation of the insect neglects the contribution of appendages to the shadow cast. The slope is significantly >0 and not significantly different from 1. These results indicate that the measured shadow area of the insect can be estimated with >91% precision using this geometric representation.

Simulated body temperature elevations, obtained using equations 1–3, are given in Figs. 2 and 3. In these figures, insect orientation is fixed at 90° (perpendicular to the sun vector), and the solar zenith angle is fixed at 45°.

When energy was expressed as the amount intercepted (watts), simulations indicate that at a given amount of energy intercepted, small insects attained a greater T_b elevation than did large insects (Fig. 2; to facilitate comparison with observations, simulation results representing the smallest and largest insects are included in Fig. 1). This probably occurs because the surface area to mass ratio increases with decreasing insect size, so that a given amount of intercepted energy heats a lesser mass of tissue in a small insect than in a large one, and thus, a small insect is heated more than a large one. In Fig. 2, the ends of each line segment represent T_b elevations at the same insolation level, for insects of a range of masses. Fig. 2 illustrates clearly that at a given level of insolation the amount of energy intercepted increases with body size, as does T_b elevation. Therefore, small body size limits the ability of the insects to elevate T_b by limiting the amount of energy intercepted and this counteracts the advantage held by a small insect at a given amount of intercepted energy.

a)

b)

Fig. 3. Idealized response surface illustrating simulated equilibrium body temperature elevation of *M. packardii* nymphs as a function of insect size and insolation (W · m^{-2}). Insects were oriented perpendicular to the solar vector; zenith angle was 45°. (a) Insect size represented by mass. (b) Insect size represented by length. The range of masses in panel "a" corresponds approximately to the range of lengths in panel "b".

Where energy was expressed as insolation (W · m^{-2}), simulated T_b elevation increased with both insect size and insolation (Fig. 3). At a given insect size, simulated T_b elevation increased linearly with insolation, but the rate of change varied with insect size. At a given insolation level, the relationship between T_b elevation and body size was nonlinear when size was expressed as mass, and approximately linear when size was expressed as length. These results are concordant with published observations that at a given level of insolation, maximum T_b elevation increases with body size (e.g., Pepper and Hastings 1952, Digby 1955, Henson 1958, Stower and Griffiths 1966, Edney 1971, Cena and Clark 1972). Comparison of these 2 sets of simulations reveals that T_b elevation increases with body size simply because the amount of en-

ergy intercepted increases with body size, and that this trend overcomes the disadvantage of large size that results from the surface area:volume ratio.

Body temperature elevation in insects has been generally expressed as function of insolation and body size. Although this approach is simple, it obscures the underlying physical determinants of T_b elevation. We believe that the approach adopted here improves significantly on this historically adopted method.

Acknowledgments

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