



CONVECTIVE HEAT LOSS AND CHANGE IN BODY TEMPERATURE OF GRASSHOPPER AND LOCUST NYMPHS: RELATIVE IMPORTANCE OF WIND SPEED, INSECT SIZE AND INSECT ORIENTATION

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Abstract—1. Grasshopper (*Melanoplus sanguinipes*, *M. bivittatus*) and locust (*Locusta migratoria migratorioides*) (Orthoptera: Acrididae) nymphs were oriented at angles to the wind stream at four wind speeds.

2. Rates of temperature and energy change due to convection were measured after compensating for Stefan–Boltzmann radiative energy exchange.

3. The rate constant for Newton's law of cooling, and the convective heat-transfer coefficient were both affected nonlinearly by insect size and wind speed, but were not significantly affected by insect orientation to the wind.

4. Comparison with published information suggests that the relationships observed apply widely within the animal kingdom. © 1998 Department of Agriculture and Agri-Food. Published by Elsevier Science Ltd. All rights reserved

Key Word Index: Convection; insect; grasshopper; locust; Orthoptera; Acrididae; body temperature; Newton's law of cooling; convective heat-transfer coefficient; biophysics

LIST OF SYMBOLS

a	Time constant	$^{\circ}\text{C}\cdot\text{s}^{-1}, ^{\circ}\text{C}^{-1}$
a_0	Time constant where $M = 1$ g and $U = 0$ $\text{m}\cdot\text{s}^{-1}$	$^{\circ}\text{C}\cdot\text{s}^{-1}, ^{\circ}\text{C}^{-1}$
A_s	Surface area of insect	m^2
b	Exponent for effect of mass on a	
c	Exponent for effect of wind on a	
c_p	Specific heat capacity	$\text{J}\cdot\text{g}^{-1}, ^{\circ}\text{C}^{-1}$
C	Rate of convective energy exchange	$\text{W}\cdot\text{m}^{-2}$
h	Convective heat-transfer coefficient	$\text{W}\cdot\text{m}^{-2}, ^{\circ}\text{C}^{-1}$
h_0	Convective heat-transfer coefficient where $M = 1$ g and $U = 0$ $\text{m}\cdot\text{s}^{-1}$	$^{\circ}\text{C}\cdot\text{s}^{-1}, ^{\circ}\text{C}^{-1}$
G	Greybody heat exchange	$\text{W}\cdot\text{m}^{-2}$
i	Exponent for effect of mass on h	
j	Exponent for effect of wind on h	
K_b	Absolute body temperature	K
K_e	Absolute environmental temperature	K
M	Insect mass	g
Q_{net}	Net rate of energy exchange	$\text{W}\cdot\text{m}^{-2}$
S	External radiation, measured on a reference plane	$\text{W}\cdot\text{m}^{-2}$
t	time	s
T_b	Body temperature	$^{\circ}\text{C}$
T_e	Air temperature	$^{\circ}\text{C}$
U	Wind speed	$\text{m}\cdot\text{s}^{-1}$

Greek Symbols

ϵ	Emissivity of grasshopper	dimensionless
σ	Stefan–Boltzmann constant	$\text{W}\cdot\text{m}^{-2}, \text{K}^{-4}$
ΔT	$T_b - T_e$	$^{\circ}\text{C}$

INTRODUCTION

Grasshoppers from a variety of taxa respond to environmental heterogeneity in ways which affect their energy balance. Tactics include shuttling between sunny and shady sites, varying orientation toward the sun, and moving vertically within near-ground gradients of temperature and wind velocity. As a consequence, their body temperatures may considerably exceed air temperature (Anderson *et al.*, 1979).

Body temperature determines the rates at which many life processes occur (Precht *et al.*, 1973); among ectotherms, these include development, fecundity, survival, mortality and feeding (Messenger, 1964; Hagstrum and Leach, 1973; Welbers, 1975; Lamb and Gerber, 1985; Lactin and Johnson, 1995). Combined, these processes make important contributions to species ecology, particularly phenology and biogeography. Consequently, understanding of

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the determinants of body temperature will be widely applicable in these and other disciplines.

The temperature of any object is determined by the rates at which it gains and loses energy; stable temperature occurs when the rates are equal and opposite (Porter and Gates, 1969). Because of their small size (Stevenson, 1985), forced convection is the most important source of energy loss in grasshoppers. This study quantifies the effects of convection on rates of energy exchange in grasshoppers.

By orienting to the sun, grasshoppers also affect their orientation to the wind, and this may affect rates of convective energy exchange (Chappell, 1983). Empirical analyses of the effect of orientation on rates of heat exchange have had contradictory results. Rates of heat loss in cylinders parallel and perpendicular to the wind stream differ by less than 10% (Thomas, 1980; Holman, 1986). Similarly, studies using live animals show that orientation to the wind has little effect on cooling rates (Digby, 1955; Muth, 1977, Kingsolver and Moffat, 1982). Studies using models of organisms reach different conclusions; these cool up to 75% faster when perpendicular to the wind than when parallel to it (Bartlett and Gates, 1967; Mitchell, 1976; Kingsolver and Moffat, 1982; Chappell, 1983). In one such study (Chappell, 1983) grasshopper models cooled significantly faster when perpendicular to the wind than when parallel to it. However, given the apparent contradiction in results obtained using models and real animal, this observation requires validation using real insects.

Our objectives in this study were: (1) to examine the effect of wind speed on the rates of convective temperature change and energy exchange in nymphal grasshoppers and locusts of different sizes; and (2) to quantify how these rates are affected by orientation to the wind stream.

MATERIALS AND METHODS

We mounted live acridid nymphs (*Melanoplus sanguinipes* (F.), *M. bivittatus* (Say) and *Locusta migratoria migratorioides* (Reiche and Fairmaire) (Orthoptera: Acrididae)) horizontally in an air stream and monitored the change in their body temperature over time (Fig. 1). Each nymph was heated and cooled while its longitudinal axis was positioned at 0, 30, 60 or 90° to the direction of wind flow. For each position, heating occurred at three wind speeds from 1 to 5 m·s⁻¹; all cooling occurred at 0 m·s⁻¹. We compensated for heat loss by greybody (Stefan-Boltzmann) radiation in the heating and cooling phases to isolate the effect of convection.

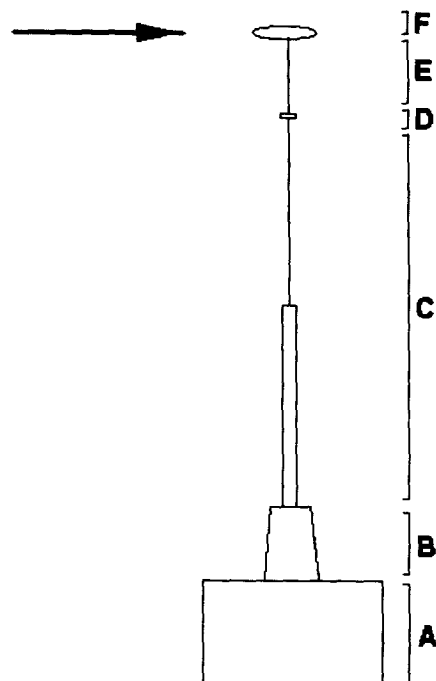


Fig. 1. Schematic diagram of method of mounting nymphs for measurement of convection. Nymphs (F) were attached by thoracic sternites to a small piece of cork (range: 2 × 2 × 1 mm–4 × 3 × 1 mm) using upholstery adhesive (EC2218[®], 3M Co., Ltd., London ON). The cork piece was attached by a insect pin (E) to the centre of a second piece of cork (4 × 4 × 2 mm) (D), which was mounted on the tip of a dissection pin (C), which was mounted vertically in a cork stopper (size 14) (B). The stopper was turned mounted on a vertical pivot in the centre of a 10 cm wooden cube (A). Mounted, the insect was ≈ 20 cm above the surface on which the wooden cube stood. Wind direction is indicated by the arrow.

Internal thoracic temperature of each nymph was monitored using a thermocouple inserted between the nymph's right meta- and meso-sternites to a depth of ≈ 2 mm. Air temperature surrounding the nymphs was sampled using four thermocouples, mounted with their tips < 2 mm from the nymph's surface. Thermocouples were placed near the head, the tip of the abdomen, and each side of the thorax. All temperatures were measured to 0.01°C using fine copper-constantan thermocouples (0.127 mm diam, model SSC-TT-T-36-36, Omega Scientific, Stamford, CT). Temperatures were output to a data logger (Model 21X, Campbell Scientific, Edmonton AB) every 3–10 s, the interval increasing with insect mass.

Wind was provided by an enclosed centrifugal fan (6.5 cm diam. × 2.8 cm) which forced air through a delivery tube (4.5 cm diam × 9 cm) containing a heating coil (1500 W). Speed and temperature of the wind stream were adjusted using a Variac. Wind speed was measured to 0.1 m·s⁻¹ using a hot-wire

anemometer (model HHF52, Omega Scientific). This trial was conducted in a closed room in which air temperature was 21–23°C and there was no measurable air movement when the fan was off.

Experimental procedure

Nymphs were mounted in the air stream, 30 cm from the opening of the delivery tube. Wind speed was established first by placing the head of the anemometer where the insect was to be located, and adjusting the Variac and the fan speed and heat controls. The fan was turned off, the anemometer replaced by a grasshopper nymph and the fan restarted. The temperature of the heated air stream surrounding the insect stabilized quickly, and the insect's body temperature equilibrated more slowly. The fan was shut off; air temperature decreased and the nymph's body temperature equilibrated with this air temperature. During both the heating and cooling phases, body temperature was monitored until it was within the range of the four measured air temperatures or its rate of change was less than $\approx 0.01^\circ\text{C}\cdot\text{s}^{-1}$. The nymph was then reoriented and the heating and cooling process was repeated. At each wind speed, this process was continued until the insect had been tested in all specified orientations. The cycles of wind adjustment and reorientation were repeated until all specified combinations had been tested. For each nymph, non-zero wind speeds were tested in random order, as were nymph orientations within wind speed.

After each trial each nymph was weighed (mg fresh body mass) and four dimensions were measured to 0.5 mm using a hand-held micrometer; these were: the maximum width of the thorax across the mesonotum (A); maximum thoracic depth (B); maximum width of the thorax across the mesosternum (C); and total length from the frons to the tip of the abdomen (D). Mean thoracic diameter was calculated as $(A + B + C)/3$. These measurements were compared with mass and length using regression.

The surface area of each insect was measured by flattening it, measuring the silhouette area by image analysis, and multiplying this area by two. The insects were dismembered to preclude overlap of body parts. Expressed tissues and gut contents were removed before area measurement.

Specific heat capacities were estimated for each insect by assuming that they are composed entirely of water and organic matter. In this case, the body specific heat capacity is the mean of that of water ($4.19\text{ J}\cdot\text{g}^{-1}\cdot^\circ\text{C}^{-1}$) and 'organic matter' ($1.92\text{ J}\cdot\text{g}^{-1}\cdot^\circ\text{C}^{-1}$), weighted by the proportions of each component in the insect (Hillel, 1980). Water and dry matter content were determined by weighing a

separate group of 63 *M. sanguinipes* nymphs (instars 1–5, fresh weights 0.00342–0.5083 g) fresh and after air drying to a constant weight at 60°C.

Analysis

Data were analysed to directly calculate the rate constant for temperature change in Newton's law of cooling (a , in $^\circ\text{C}\cdot\text{s}^{-1}\cdot^\circ\text{C}^{-1}$), and the convective heat-transfer coefficient (h , in $\text{W}\cdot\text{m}^{-2}\cdot^\circ\text{C}^{-1}$). All symbols used in the following presentation are listed and defined in the list of symbols.

Analysis compensated for the effects of greybody radiation on rates of temperature change. In the present experimental design, greybody radiation always resulted in energy loss. Net greybody radiation exchange with the surroundings ($\text{W}\cdot\text{m}^{-2}$) was calculated by applying the Stefan–Boltzmann law.

We neglect the effects of evaporation, metabolic heat production, and heat conduction along the thermocouple wires, because they have very small effects in our system. Evaporative cooling is minimal in grasshoppers, except in some unusually large species (Prange, 1990), and even in such species, maximum evaporative temperature loss between 25 and 40°C was $\approx 0.001^\circ\text{C}\cdot\text{s}^{-1}$. In our experiment, this maximum rate was $< 1\%$ of measured temperature change under such conditions. (Note: at higher temperatures, water loss may be much greater due to disruption of the waxy cuticle; Beament, 1959). Grasshopper nymphs are ectothermic, and metabolic heat production is negligible (Heinrich, 1993). We also calculated that heat conduction along thermocouple wires was negligible.

Estimation of parameters for each insect

Time constant. Data were first analysed by applying Newton's law of cooling to the net rate of convective temperature change (i.e., the measured change adjusted for the greybody exchange), in which an object's rate of temperature change is proportional to the difference (ΔT) between the object's surface temperature (i.e., body temperature, T_b) and that of the surrounding medium (T_a):

$$\frac{\partial \Delta T}{\partial t} = a \Delta T - \frac{GA_s}{Mc_p}, \quad (1)$$

where a is the time constant (i.e., the inverse of the time required for ΔT to change from any value to $1/e$ times that value) and $G = \epsilon \sigma (K_b^4 - K_c^4)$, i.e., the rate of energy exchange with the surroundings by greybody (Stefan–Boltzmann) radiation. A value of 0.94 was used for ϵ (Campbell, 1977). Environmental temperature (K_c) was assumed to equal room temperature outside the air stream. The value of a

was estimated for each insect under each set of conditions by least-squares linear regression on a rearranged version of equation (1) [equation (2)].

$$\frac{\partial \Delta T}{\partial t} + \frac{GA_s}{Mc_p} = -a\Delta T. \quad (2)$$

After each change in wind speed, air stream temperature took a short time to equilibrate, and the interval required for this varied inversely with wind speed. Change in nymphal body temperature was monitored only after the air temperature had equilibrated after the wind source was turned on or off. For each insect at each combination of orientation and wind speed, the time to air temperature equilibration was calculated by estimating the time constant and equilibrium value of the curve describing change in air temperature over time, then solving algebraically for the time required for the difference between air temperature and the equilibrium value to reach 1% of the initial difference. This interval ranged from ≈ 0 s at wind speed = $5 \text{ m}\cdot\text{s}^{-1}$, to ≈ 40 s at $0 \text{ m}\cdot\text{s}^{-1}$. At least 24 data points remained for each insect at each combination of orientation and wind speed.

Convective heat-transfer coefficient. Data were also analysed to estimate the convective heat-transfer coefficient (h , in $\text{W}\cdot\text{m}^{-2}\cdot^\circ\text{C}^{-1}$):

$$C = -h\Delta T - G. \quad (3)$$

The quantity C was calculated from our data as $(\partial\Delta T/\partial t)\cdot(Mc_p/A_s)$. The value of h was estimated for each insect under each set of conditions by rearranging equation (3) to an analogue of equation (2), and applying linear regression.

Relationships of h and a to orientation, species, size and wind speed. The relationships of the estimates of h and a to insect species, insect size, and the orientation of the nymph were examined using Analysis of Covariance (PROC GLM, SAS Institute, 1990). For this analysis we considered only cases where wind speed was $> 0 \text{ m}\cdot\text{s}^{-1}$ because orientation is meaningless where wind speed = 0. For this analysis, wind speed was log-transformed to linearize trends.

For subsequent analyses, estimates of a and h were obtained for each nymph at each wind speed by pooling data over orientations at each wind speed. The rate of temperature change of an object varies with wind speed and the size of the object (Mitchell, 1976), and thus the parameters a and h are actually bulk values which include the contributions of size and wind speed (U). Therefore, the rate constant (a) can be partitioned:

$$\frac{\partial \Delta T}{\partial t} = -a_0 \text{ mass}^b(0.1 + U)^c\Delta T - \frac{GA_s}{Mc_p}, \quad (4)$$

where a_0 is the time constant of a 1-g nymph at $U = 0 \text{ m}\cdot\text{s}^{-1}$.

Similarly, h can be partitioned:

$$C = -h_0 \text{ mass}^i(0.1 + U)^j\Delta T - G. \quad (5)$$

In equation (4) and equation (5), $0.1 \text{ (m}\cdot\text{s}^{-1})$ is added to wind speed to account for cooling by passive (natural) convection (Gates, 1980).

Substituting the right-hand side of equation (1) for the left-hand side of equation (4), cancelling common variables and extracting the logarithm of both sides results in a linear equation [equation (6)]:

$$\ln(a) = \ln(a_0) + b\ln(M) + c\ln(0.1 + U), \quad (6)$$

where a is the time constant from equation (2), and a_0 , b and c are as in equation (4). Similarly,

$$\ln(h) = \ln(h_0) + i\ln(M) + j\ln(0.1 + U). \quad (7)$$

In the final step of the analysis, parameter estimates were obtained by linear regression using equation (6) or equation (7).

The length of an insect is often easier to measure than its mass. Therefore, we repeated all analyses, using nymph length as the measure of size.

Comparison with published results. To render our results comparable with some of the reports from the literature, we also analysed our cooling rate and heat loss data without adding $0.1 \text{ m}\cdot\text{s}^{-1}$ to wind speed [equations (4)–(7)]. We consider this a subordinate analysis because results imply unrealistically that no convective cooling occurs when wind = 0.

RESULTS

This trial was conducted on 30 nymphs, 10 of each species. Mass varied from 0.0284 to 1.938 g, and length from 8.5 to 40.0 mm. Typically, in a given instar, *M. sanguinipes* nymphs were the smallest and *L. migratoria* the largest. Grasshopper surface areas ranged from 71.6 to 1785.3 mm².

Insect dimensions and surface areas were related allometrically to mass (Table 1). Mean thoracic diameter (T) was related linearly to insect length (D) by the significant relationship $T = 0.356 + 0.241\cdot D$, with $F_{1,28} = 843$ and $r^2 = 0.9678$; standard errors were 0.166 for the intercept and 0.008 for the slope.

Proportional water content averaged 0.755 with a standard error of 0.0237. The corresponding estimate of specific heat capacity is $3.63 \text{ J}\cdot\text{g}^{-1}\cdot^\circ\text{C}^{-1}$ (Hillel, 1980). This estimate is similar to the value commonly used, i.e., $3.42 \text{ J}\cdot\text{g}^{-1}\cdot^\circ\text{C}^{-1}$ (Heinrich, 1993).

The time constant did not vary among species, either as a main effect or by interaction with $\ln(\text{wind})$ (both $P > 0.2$); it was also not significantly affected by the orientation of the nymph to the wind stream,

Table 1. Allometric relationships among insect dimensions

Dimension	Intercept		Slope		$F_{1,28}$	r^2
	Est.	S.E.	Est.	S.E.		
Thorax diameter (mm)	-4.795	0.0287	0.3420	0.0139	609	0.9560
Length (mm)	-3.417	0.0282	0.3655	0.0136	722	0.9627
Surface area (mm ²)	-6.648	0.0661	0.8000	0.0319	629	0.9573

Parameter estimates and regression statistics from regressions of $\ln(\text{dimension})$ on $\ln(\text{mass})$.

either alone or through interaction with $\ln(\text{wind})$ (both $P > 0.14$) (Fig. 2).

Similarly, the convective heat-transfer coefficient did not vary among species either as a main effect or by interaction with $\ln(\text{wind})$ (both $P > 0.07$); it was also not significantly affected by the orientation of the nymph to the wind stream, either alone or through interaction with $\ln(\text{wind})$ (both $P > 0.09$). Because of these results, the effects of species and orientation to the wind were subsumed into the error term in subsequent analyses.

Parameter estimates

The time constant and the convective heat-transfer coefficient both decreased logarithmically as insect size increased and increased logarithmically as wind speed increased (Tables 2 and 3; Figs 3–6). In Figs 3 and 4, cooling rate or heat exchange rate data are presented along with curves representing best fits at each wind speed, for the time constant (vs mass in Fig. 3a; and vs length in Fig. 3b) or the convective heat-transfer coefficient (vs mass in Fig. 4a; and vs length in Fig. 4b). The data points are more narrowly distributed around the regression curves when insect size is represented by mass than by length, an observation reflected in the comparative r^2 values for

equations (6) and (7) (Tables 2 and 3). The difference in precision results from the imperfect correlation between mass and length (Table 1). The comparative precision of the regressions indicate that mass is a more appropriate dependent variable for this analysis than is length. Figures 5 and 6 are idealized pseudo-three-dimensional representations of the surfaces relating the time constant or convective heat-transfer coefficient to wind speed and insect mass or length.

Addition of 0.1 m s^{-1} to the wind speed resulted in a 15–20% change in the exponents relating rates of temperature change or heat exchange to wind or insect size. Where 0.1 m s^{-1} was added to wind speed the F and r^2 values are greater than in the case where this was not done; therefore, addition of 0.1 m s^{-1} improved the fit of the model to the data. Consequently, we conclude that adding 0.1 m s^{-1} is the superior method. Furthermore, adding the scalar

Table 2. Time constant for change of body temperature (a , in $^{\circ}\text{C s}^{-1} \cdot ^{\circ}\text{C}^{-1}$)

Parameter	Measure of insect size			
	Mass		Length	
	Estimate	S.E.	Estimate	S.E.
Wind + 0.1				
$\ln(a_0)$	-5.2752	0.04830*	0.3859	0.2085†
b	-0.6099	0.02410	-1.6119	0.0723
c	0.5697	0.01569	0.5689	0.0174
Wind				
$\ln(a_0)$	-5.0246	0.07206‡	-0.1138	0.2250§
b	-0.5311	0.02432	-1.4006	0.0747
c	0.4830	0.05162	0.4913	0.0587

Estimated parameters of the relationship describing influences of insect size and wind speed [equation (6) in the text], with and without addition of 0.1 to wind speed to account for passive convection.

* $a_0 = 0.005117$; detransformed 1 S.E. interval: 0.004876–0.005370; $F_{2,106} = 944$; $r^2 = 0.9469$.

† $a_0 = 1.471$; detransformed 1 S.E. interval: 1.194–1.812; $F_{2,106} = 753$; $r^2 = 0.9342$.

‡ $a_0 = 0.006574$; detransformed 1 S.E. interval: 0.006117–0.007065; $F_{1,76} = 284$; $r^2 = 0.8820$.

§ $a_0 = 0.8924$; detransformed 1 S.E. interval: 0.7126–1.1176; $F_{1,76} = 211$; $r^2 = 0.8474$.

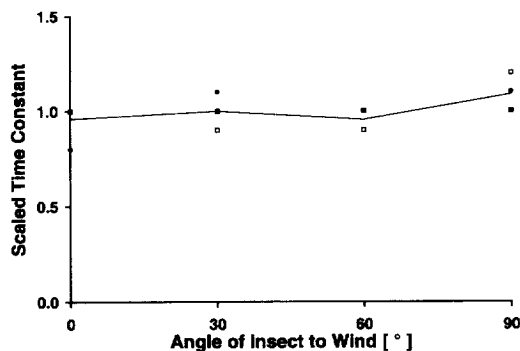


Fig. 2. Time constants for grasshoppers at four orientations to the wind stream at each of four wind speeds (U , in m s^{-1}). At each wind speed, the constant is scaled to a proportion of the mean value at that speed.: $\bullet$, $U = 1.5$; $\square$, $U = 3$; $\blacksquare$, $U = 5.0$. Solid lines join mean scaled conductances over wind speeds, weighted by the number of observations.

Table 3. Convective heat-transfer coefficient (h , in $W \cdot m^{-2} \cdot ^\circ C^{-1}$) in grasshopper and locust nymphs

Parameter	Measure of insect size			
	Mass		Length	
	Estimate	S.E.	Estimate	S.E.
Wind + 0.1				
$\ln(h_0)$	2.6790	0.05852*	6.2682	0.2252†
i	-0.3798	0.00291	-1.0254	0.0782
j	0.5659	0.01850	0.5637	0.0184
Wind				
$\ln(h_0)$	2.9476	0.07367‡	5.8373	0.2163§
i	-0.3072	0.02645	-0.8273	0.0718
j	0.4534	0.05613	0.4582	0.0564

Estimated parameters of the relationship describing influences of insect size and wind speed [equation (7) in text] with and without addition of 0.1 to wind speed to account for passive convection.

* $h_0 = 14.571$; detransformed 1 S.E. interval: 13.742–15.449; $F_{2,106} = 530$; $r^2 = 0.9068$.

† $h_0 = 527.53$; detransformed 1 S.E. interval: 421.16–660.77; $F_{2,106} = 533$; $r^2 = 0.9072$.

‡ $h_0 = 19.061$; detransformed 1 S.E. interval: 17.606–20.517; $F_{2,106} = 101$; $r^2 = 0.7265$.

§ $h_0 = 342.85$; detransformed 1 S.E. interval: 276.17–425.64; $F_{2,106} = 99$; $r^2 = 0.7235$.

gives more realistic output, because it acknowledges that convective cooling occurs when $U = 0 \text{ m} \cdot \text{s}^{-1}$.

DISCUSSION

Orientation of the nymph to the wind did not affect the time constant or the convective heat-transfer coefficient. This observation is consistent with published observations using real organisms and contradicts results obtained using models. There are at least three possible explanations for this lack of orientation effect: (1) that thoracic temperature may not adequately represent that of the entire body; (2) that due to the small size and composition of the insect, internal transfer of heat may be so rapid that measurable temperature gradients cannot establish; or (3) that the appendages affect air flow over the insect (Kingsolver and Moffat, 1982), resulting in the insect being surrounded by a roughly spherical mass of turbulent air such that regardless of how energy is transferred through this mass, the rate would be little affected by the orientation of this spheroid to the wind.

The first suggested explanation would only occur if the thorax is effectively isolated from the other major body sections (tagmata) by internal barriers to heat flow. This is unlikely, because in crickets, *Conocephalus dorsalis* (Orthoptera: Tettigoniidae) body temperatures remain uniform throughout the body

(Schmaranzer and Stabentheiner, 1991); thus, heat flows freely among the tagmata in this species and presumably other orthopterans. Since our experimental insects were immersed in the air stream, they were heated uniformly, and the apparent free exchange of heat among the tagmata suggests that the isolation of the thorax which is necessary to this explanation, does not occur. The second and third possibilities are both plausible, and not mutually exclusive.

Orientation to the wind can be ignored when calculating rates of convective heat exchange in grasshopper nymphs. Given that convective heat exchange is also independent of orientation in butterflies (Kingsolver and Moffat, 1982) and lizards (Muth, 1977), which are very different taxonomically and geometrically from grasshoppers, this conclusion seems widely applicable. However, physical models of butterflies (Kingsolver and Moffat, 1982) and lizards (Bartlett and Gates, 1967) do show orientation effects: they cooled significantly faster when perpendicular to the wind than when parallel to it. The different results of studies using models and real subjects may invalidate results of convection studies using models.

The time constant and the convective heat-transfer coefficient both responded nonlinearly to changes in wind speed and body size (i.e., mass or length).

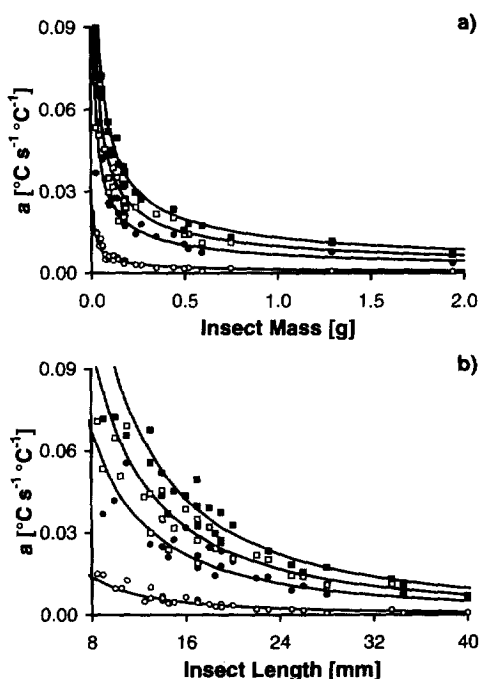


Fig. 3. Time constant vs body size. Symbols represent different wind speeds (U , in $\text{m} \cdot \text{s}^{-1}$): $\circ$, $U = 0$; $\bullet$, $U = 1.5$; $\square$, $U = 3$; $\blacksquare$, $U = 5$. Curves are predictions from equation (6); from bottom to top, these correspond to $U = 0$, $U = 1.5$, $U = 3$ and $U = 5$. (a) Size represented by mass. (b) Size represented by length.

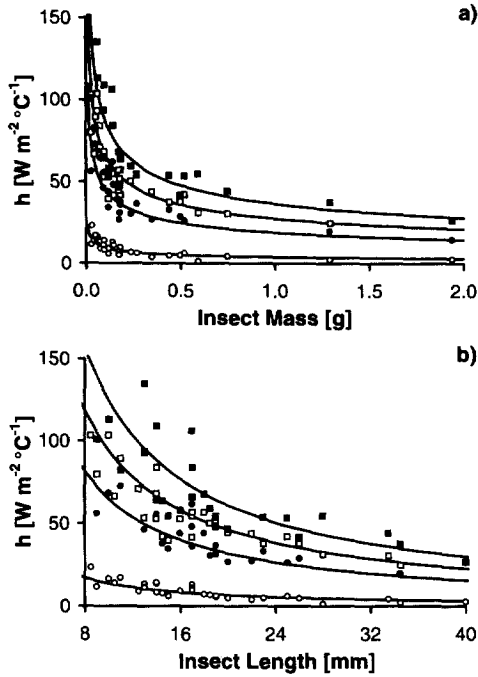


Fig. 4. Convective heat-transfer coefficient vs body mass. Symbols and overlain curves as in Fig. 2. (a) Size represented by mass. (b) Size represented by length.

However, the effects of insect size and wind speed on the Newtonian rate and the convective heat-transfer coefficient did not differ significantly among species.

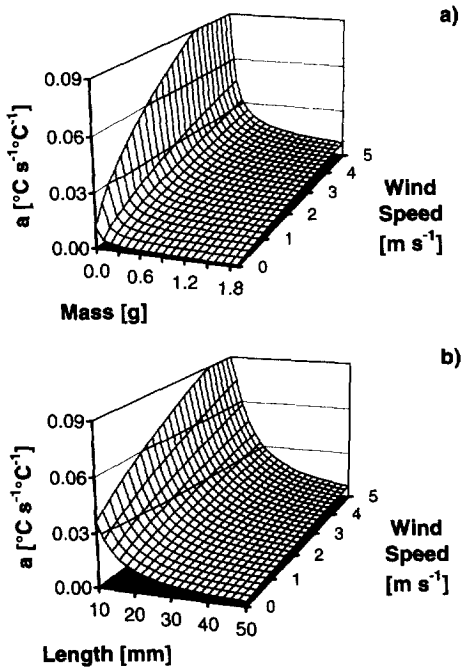


Fig. 5. Idealized response surfaces presenting relationship of time constant to insect mass and (wind speed + 0.1 m s^{-1}). (a) Size represented by mass. (b) Size represented by length.

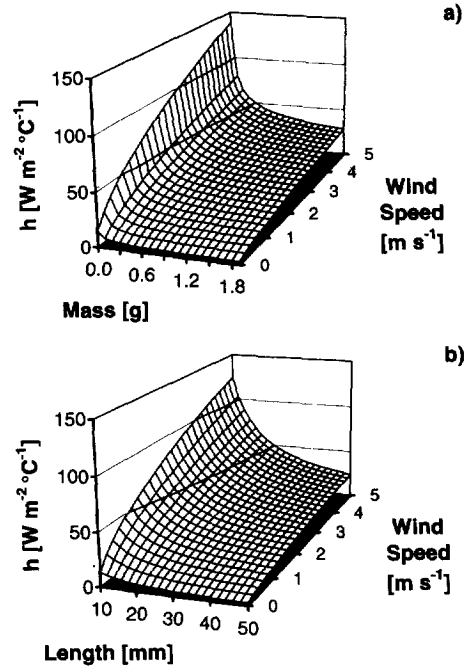


Fig. 6. Idealized response surface presenting relationship of convective heat-transfer coefficient to insect mass and (wind speed + 0.1 m s^{-1}). (a) Size represented by mass. (b) Size represented by length.

This result indicates that the biophysical mechanism which controls the rates of temperature change and energy exchange are approximately uniform among the species tested. Further, the range of body sizes encountered in this study covers most of the range observed in the Acrididae; given the similarity of body shapes within this taxon, these results may apply widely within the family.

Comparison with published results

Wind effects. The time constant and the convective heat-transfer coefficient both increased as an exponential function of increasing wind speed, whether or not 0.1 m s^{-1} was added to wind speed. Our estimates for the exponent of the relationship was between 0.56 and 0.57 where 0.1 m s^{-1} was added, and between 0.45 and 0.49 otherwise. These exponents generally agree with published values in a variety of other animals which range from 0.466 to 0.78 (Mitchell, 1976). Mitchell suggests using 0.6.

Size effects. Exponent estimates for the effect of size on rates of cooling and energy exchange were also affected by adding 0.1 m s^{-1} to wind speed (Tables 2 and 3). Published reports have expressed animal size as mass, and results have been expressed in terms compatible with our time constant estimates; these were all measured in still air, so 0.1 was not added to wind speed. In moths, time constants for post-flight cooling in moths scale as the -0.469 and

– 0.489 power of thoracic mass in *Cecropia* moths and Hawk moths (Lepidoptera: Saturniidae and Sphingidae), respectively (Bartholomew and Epting, 1975a, 1975b). In birds and mammals, Herreid and Kessel (1967) presented temperature change in birds and mammals as ‘conductance’ ($\text{cal}\cdot\text{g}^{-1}\cdot\text{h}^{-1}\cdot^{\circ}\text{C}^{-1}$); we converted these to time constants. In birds, the time constant scaled very closely to $\text{mass}^{-0.5}$ (S.E. ≈ 0.02), with exponents differing slightly depending on whether feathers and skin were present. In specimens of 24 mammal species, the time constant scaled as $\text{mass}^{-0.52}$ (S.E. = 0.05). All of these exponents agree well with our estimates where we did not add $0.1\text{ m}\cdot\text{s}^{-1}$ to wind speed (i.e., ~ -0.49).

The intercept term in the Newtonian cooling relationship. The intercept parameter $\ln(a_0)$ in equation (6) represents the cooling rate of an organism weighing 1 g at a wind speed of $0\text{ m}\cdot\text{s}^{-1}$. The value obtained in the present study (-5.2752) was very similar to that observed in birds with skin and feathers removed (-5.302 ; Herreid and Kessel, 1967), but higher than that observed in birds with skin and feathers in place (-6.510) and in mammals with pelage intact (-6.381) (Herreid and Kessel, 1967). This comparison of intercepts indicates that the lower intercept in mammals is due to the presence of insulation. The intercepts of this regression in saturniids (-6.42) and sphingids (-6.41) (Bartholomew and Epting, 1975a), which are well insulated, are also very similar to those of the insulated birds and mammals.

Summary of comparisons. Our results indicate that wind-dependent cooling rates of grasshoppers vary with wind speed, as $\sim (0.1 + U)^{0.6}$ or $\sim U^{0.5}$. This consistent exponent suggests that the value is approximately constant, possibly as a consequence of the relatively constant physical properties of air and animal tissues. Published values of the exponent for the effect of mass on the time constant agree well with our estimates where appropriate comparison was used (i.e., with or without addition of $0.1\text{ m}\cdot\text{s}^{-1}$ to wind speed). This agreement is not taxonomically restricted. Although less compelling, some evidence also suggests that the intercept term of the Newtonian cooling relationship is similar among uninsulated animals.

These similarities suggest that the cooling relationship $\partial\Delta T/\partial t = a_0\cdot\text{mass}^b\cdot(0.1 + U)^c$ may be broadly applicable among terrestrial animals, with $b \approx -0.5$, $c \approx 0.6$, and $\ln(a_0) \approx -5.2$ in uninsulated organisms and lower in the presence of insulation. Other authors have suggested widespread similarity in b (Kleiber, 1972) and c (e.g., Mitchell, 1976) among such animals, but the suggestion of broad applicability of $\ln(a_0)$ appears novel. Since a_0 corresponds to

the cooling rate of an organism of 1 g in air at wind speed = 0 this possibility is plausible, considering that terrestrial animals are all composed of similar proportions of water and organic contaminants.

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