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# HOT BUGS: BODY TEMPERATURE OF INSECTS IN SUNSHINE


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FACTORS AFFECTING THE TEMPERATURE EXCESS OF INSECTS IN SUNSHINE

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(*Received 1 April 1954*)

(I) INTRODUCTION

The temperature of an insect is of paramount importance in determining its activity. When heated by the sun its temperature is not the same as that of the air but is greater by an amount which we will call the temperature excess. As activity is so dependent on temperature it is of considerable interest to know more about the way in which the various factors operate to control this temperature excess.

The direct field observations so far made on the temperature excess of an insect in the sunshine apply to large forms such as the locust (Buxton, 1924; Strelnikov, 1936; Kennedy, 1939; Gunn, Perry, Seymour, Telford, Wright & Yeo, 1948; Parry, 1951). Calculations such as those by Parry (1951), although they yield quite a reasonable answer for an insect the size of a locust at a considerable wind speed, involve a number of assumptions. There is reason to believe that certain of these would not hold good for most insects of temperate lands which are much smaller, and which are found when resting in positions with very low wind velocities. These wind velocities are certainly below 1 m./sec. and often below 0·1 m./sec. (see Stocker, 1928; Geiger, 1950).

This paper describes laboratory experiments on the temperature excess of insects and plasticine spheres carried out under known conditions similar to those found in microclimatic conditions in the field, with a view to finding the temperature excess to be expected under natural conditions, and to elucidating the way in which the factors work at small size and low wind speed.

Now it can be shown that for a small physical body similar to an insect the temperature excess varies directly with the radiation strength; with the absorptivity (which depends on the spectral composition of the radiation and on the colour and characteristics of the body); with a fractional power of the size, and inversely with a fractional power of the wind velocity. Metabolism and evaporation are practically negligible in the resting insect. Uncertainty arises concerning the relations between temperature, wind and size, for at small size and low wind speeds bodies tend to develop their own convection currents and to be controlled by the laws of natural convection rather than forced convection. It is to be expected that small insects in their natural habitat lie in the region of transition between these two types of flow. Of the factors involved in heat loss by convection, variation in the viscosity, density and conductivity of the air may be neglected as their effects over

*Michael May writes about Peter S. B. Digby's 1955 publication on factors affecting the temperature excess of insects in sunshine.*

It is always tempting to see the past as a dark and primitive age or a golden and heroic one. Peter Digby's classic paper, after half a century, can perhaps be viewed from both perspectives. Either way it represents, if not a turning point, certainly a substantial stride toward understanding how and why many insects interact with their thermal environment and even manage surprising feats of thermal homeostasis. Interestingly, this was, as far as I know, Digby's only foray into the field of thermal biology of insects – his later work focused largely on electrochemical properties of biological materials.

Appreciation of the correlation of insect activity with temperature surely predates historical records, and a rudimentary understanding of their behavioral responses to sunlight existed in biblical times (May, 1979). Efforts to measure the body temperature of insects date to early in the 19th century (cited by Heinrich, 1981), and by the late 1930s a number of workers had investigated body temperature of some large insects, especially desert and migratory locusts. Nevertheless, techniques were relatively crude and quantitative understanding of the role of insect behavior and internal or environmental heat sources correspondingly poor. In the post-War period, however, improved instrumentation (and perhaps also an accelerating sense that much could be learned by investigating organisms as physical systems) set the stage for more sophisticated examination of these phenomena. Also, impelled perhaps by similar trends, studies of microclimate, especially the publication of Geiger's (1950) influential book, made possible a better understanding of the physical milieu that insects experience.

In 1951, D. A. Parry had estimated, and published in *The Journal of Experimental Biology*, body temperatures of moderate- to large-sized insects based on physical principles of heat exchange and measurements of artificial bodies under controlled conditions. This provided much useful information, but it was not until Digby's work that comparably careful work was applied to actual living or recently killed insects over a wide size range. Although still confined to a laboratory setting, Digby went to considerable lengths to simulate reasonable natural conditions of radiation intensity, spectral distribution and wind velocity (although without the level of turbulence expected in the field). Each of these has effects that are easily predictable qualitatively – body temperature will be positively correlated with radiation intensity, be affected by spectral composition in a way determined by the colour of the insect, and be reduced as wind (or flight) speed increases; the quantitative effects, however, were still largely unknown. Taking advantage of fine-gauge thermocouples then available, Digby was able to measure accurately the thoracic temperature of insects as small as houseflies and the variation of temperature across the thorax in slightly larger flies. He used the clever expedient of using wing-beat frequency as an apparently accurate surrogate for body temperature in *Drosophila*, although this was also slightly worrisome because it introduced the variability inherent in an intact organism.

Digby presented his data in terms of temperature excess (a term that I believe he coined), i.e. the difference between body temperature and ambient air temperature. Most of his results are unsurprising and are largely taken for granted today. It is well to remember, though, that heat exchange of oddly shaped and varicolored objects in natural or even laboratory environments is complex enough to make empirical evaluation essential. Many assumptions about thermal properties of insects rest on Digby's research. He showed, for example, that in general temperature excess increases linearly with radiation intensity. However, this relationship can change at combinations of low wind speed and/or large body size that result in a significant shift from forced convection (heat loss due to wind flowing over the body) to free convection (heat loss due to buoyancy of air heated at the body surface). Digby found that the spectral composition of radiation within the range of natural sunlight had a negligible effect on temperature excess. Colour of the cuticle also had surprisingly little influence, given the visually obvious differences in hue and apparent reflectivity among the cuticles of different insects. Digby concluded that this was largely because about 50% of solar radiation lies in the near infrared range, where most cuticles absorb nearly all radiation. Thus, even relatively brightly coloured insects are effective reflectors only within a fraction of the 40–50% of sunlight in the visible range (reflectivity in the ultraviolet is variable but not necessarily correlated with visible colour).

One interesting and often overlooked finding was that blackening the insect's cuticle could actually reduce temperature excess at the body core, probably because more radiant heat was absorbed near the body surface and thus was lost more readily by convection. Although Digby did not pursue the issue in this context, the phenomenon is likely to affect the relative importance of metabolic and radiative heating of large insects flying in sunshine. He also showed that, when insects are heated in sunlight to equilibrium and then induced to begin flying, temperature excess increases much less than predicted by a simple additive model, most likely owing to high rates of convective and evaporative heat loss from the already warm body surface and the tracheae just beneath it.

Body size and shape can have strong effects on temperature excess in insects, and these, too, engaged Digby's attention. These variables proved to interact in interesting ways. As expected, he found that larger insects heated less rapidly but to substantially higher equilibrium body temperature than small ones under the same conditions. All insects tended to attain higher temperature excess than similarly sized plasticine spheres, and flies and wasps, especially larger specimens, became warmer than locusts of similar diameter. Digby attributed these differences mostly to the shielding effects of the insect's head and abdomen, which would trap a layer of unstirred warm air over the anterior and posterior surfaces of the thorax, leading to a reduction of convective cooling of the thorax. However, he probably dismissed too readily the additional effects of hairs covering the body of insects such as bees, which also trap warm air near the body, as clearly shown by Church (1960b) and others; thus hairier insects might reach higher temperature excess when exposed to sunlight and a moderate wind than similar sized smooth insects.

When Digby turned his attention to the effects of wind velocity on temperature excess, he found that elongate species were cooler if turned perpendicular to the wind, a feature that subsequently was shown to influence body orientation of locusts in the field (e.g. Chapman, 1959; Waloff, 1963). At moderate or high wind velocity, he found that temperature excess was proportional to (velocity)$^{-2}$, although at very low speeds the relative increase in importance of free convection reduced the influence of wind speed.

Seen from the standpoint of 2005, with its enormous increase in miniaturization, computerization and ease of use of equipment, the most heroic aspect of Digby's work was the care and effort that he put into construction and calibration of apparatus. Of course in this he was not different from many other researchers of the day, and in any case the nature of the research probably makes it attractive to tinkerers. Nonetheless, it required that accuracy not be taken for granted but painstakingly verified and that the physical principles underlying the operation of instruments be well understood. A good many of our boxes have gone black since then, with corresponding gains in convenience and productivity, to be sure, but possibly at the cost of some understanding of just what our electronic marvels are really doing – not that I'd go back to the good old days of 1955, but I am reminded that most of us know more and more about less and less.

Digby's work set the stage for a surge of interest in, as well as improved methods for, the study of the reciprocal interaction of temperature with the behavior and ecology of large insects (e.g. Church, 1960a,b; Stower and Griffiths, 1966; and see references cited above). It was not until Heath's development of the 'grab and stab' technique (Heath, 1967), using portable thermistor or thermocouple thermometry, that abundant and fairly reliable field data on insect body temperature became available. Nonetheless, Digby's JEB classic surely deserves credit for providing an important section of the foundation for work that, over the next three decades or more, added several new chapters to our understanding of thermal ecology and body temperature regulation in the world's most successful organisms.

A PDF file of the original paper can be accessed online: http://jeb.biologists.org/cgi/content/full/208/14/2623/DC1

10.1242/jeb.01724

### References

**Chapman, R. F.** (1959). Field observations of hoppers of the red locust (*Nomadacris septemfasciata* Serville). *Anti-Locust Bull.* **33**, 1-51.
**Church, N. S.** (1960a). Heat loss and the body temperature of flying insects. I. Heat loss by evaporation of water from the body. *J. Exp. Biol.* **37**, 171-185.
**Church, N. S.** (1960b). Heat loss and the body temperature of flying insects. II. Heat conduction within the body and loss by radiation and convection. *J. Exp. Biol.* **37**, 186-213.
**Digby, P. S. B.** (1955). Factors affecting the temperature excess of insects in sunshine. *J. Exp. Biol.* **32**, 279-298.
**Geiger, R.** (1950). *The Climate Near the Ground*. Cambridge, MA: Harvard University Press.
**Heath, J. E.** (1967). Temperature responses of the periodical '17-year' cicada, *Magicicada cassinii*. *Amer. Midl. Nat.* **77**, 64-76.
**Heinrich, B.** (1981). *Insect Thermoregulation.* New York: John Wiley.
**May, M. L.** (1979). Insect thermoregulation. *Ann. Rev. Ent.* **24**, 313-349.
**Parry, D. A.** (1951). Factors determining the temperature of terrestrial arthropods in sunlight. *J. Exp. Biol.* **28**, 445-462.
**Stower, W. J. and Griffiths, J. F.** (1966). Body temperature of the desert locust. *Ent. Exp. Appl.* **9**, 127-178.
**Waloff, Z.** (1963). Field studies on solitary and traniens desert locusts in the Red Sea area*. Anti-Locust Bull.* **40**, 1-93.

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