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Thermoelectric Effect in Hornet (*Vespa orientalis*) Silk and Thermoregulation in a Hornet's Nest

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The silk caps of the pupae of the Oriental hornet (*Vespa orientalis*, Vespinae, Hymenoptera) were measured for spontaneous electric current flow as a function of temperature. The measurements were made in the dark, within a range of biological temperatures. A clear correlation was detected between temperature rise and the increase in electric current forming in the silk. Thus at the temperature associated with maximal current, namely, 28–31°C, the electric current reached hundreds of nAmp whereas at 5°C the current was merely dozens of nAmp. Interestingly, the temperature range associated with optimal currents is also identical to the optimal temperature extant in the hornet nest thus enabling proper development of the colony. In the Discussion section, an attempt is made to explain the thermoelectric mechanism in pupal silk and its contribution, as thermometer and thermostat, to thermoregulation of the individual pupae, each of which is an independent thermal unit. The thermoregulation here is compared with the mode of action of heating pipes in industry. For further comparison, silk cocoons of the silkworm *Bombyx mori* were also measured, but while the readings on silkworm silk were comparable to those on hornet silk, they were lower by one order of magnitude.

Silk Hornets Silkworm Thermoelectric effect Peltier effect Social wasp pupae Dark conduction Organic semiconductors Wet–dry cooling Joule heating

INTRODUCTION

Warming, ventilation and air conditioning are all features of environmental engineering but are also very well known aspects of many groups of social insects, especially those that build combs to rear their brood. The production of healthy brood and adults in a social wasp's nest is markedly influenced by temperature. It is essential for the hornets to be kept warm, otherwise malformed adults emerge (Ishay and Ruttner, 1971). The temperature in a nest is usually maintained at 28–32°C and this narrow range is constant for many species of wasps and hornets, especially those that live in temperate regions. The role of adult hornets in thermoregulation of the nest has long been known, entailing the attachment of water droplets upon the silk caps, to cool the interior of the nest, ventilation to aerate the nest, and warming by blowing warmer air from the tracheal openings towards the pupae in their cocoons or even on pupae that have been extracted from their cocoons. In an experiment intended to ascertain whether the task of air-conditioning the nest rests on the adult hornets alone (Ishay and Ruttner, 1971), the adult population was removed from a nest of *Vespa crabro* reared in the laboratory and the nest was monitored over the next 3 days for any changes in its temperature. It was found that during the first 30 h, the brood manages to retain the temperature at 28–30°C, just as in the presence of adult hornets, and this is in contrast to a temperature of only 22–24°C in an adjacent, vacant breeding box. With the passage of another 30 h, however, they can only maintain the temperature at 26–28°C and subsequently, there is even a further drop to a mere 2°C above that in the empty breeding box. The findings of this experiment indicated that the various stages of hornet brood also played a role in thermoregulation of the nest. Among the brood stages, it is believed that the larvae create heat by activating their muscles, including the muscular effort involved in sounding the "Hunger Signal" (Schaudinischky and Ishay, 1968). Such activity is absent in the pupal stage, which raises the question as to whether the pupae possess another means of assessing the ambient temperature and modifying it according to its needs. In this connection, it is noteworthy that what characteristically sets the pupae apart from the rest of the population in the nest is the silk envelope whose

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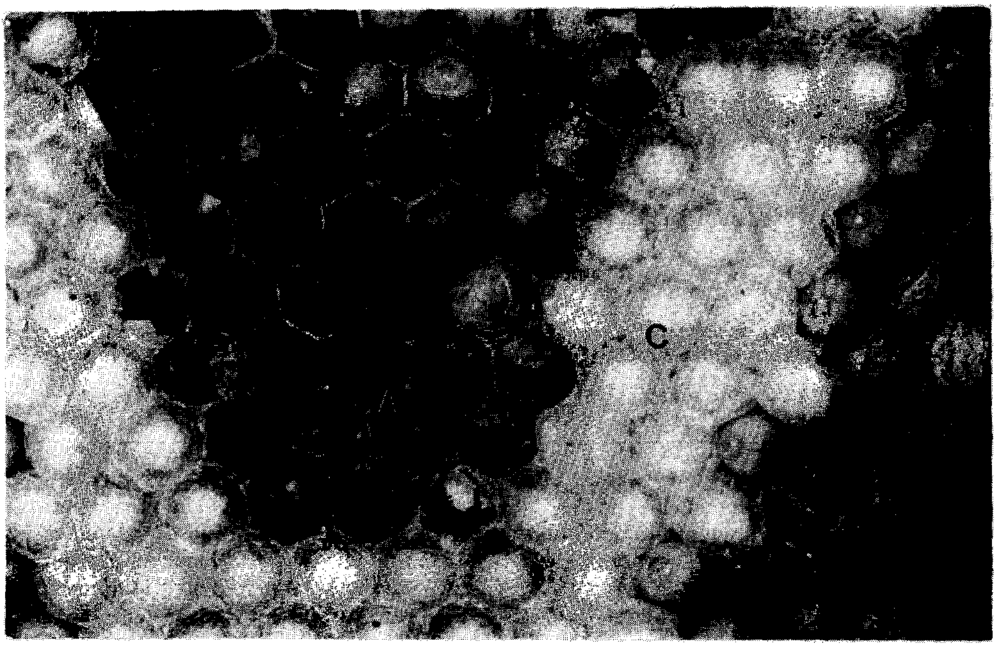

FIGURE 1. A view from below of a piece of a comb of the Oriental hornet *Vespa orientalis*. The various brood stages can be seen: (A) eggs and larvae in 1–3 instars; (B) lavae of instars 4–5 (they already occupy the entire cell volume); and (C) pupae encased in their cocoons. The white sealings of the cocoon cell openings are the so-called silk caps. Such silk caps were measured in this work after being removed from the cocoon.

dome, or cap, protrudes from the comb cell housing the pupae and seals its outlet (Fig. 1). In previous investigations, we found that the silk caps are luminescent (Benshalom-Shimony and Ishay, 1990), which is similar to the luminescence of the hornet cuticle (Ishay *et al.*, 1987). Furthermore, the silk caps display maximal voltage and current at a maximal relative humidity (RH) (Ishay *et al.*, 1991; Ishay and Ben-Shalom, 1992). The various electric properties of the pupal silk of hornets have been elucidated and summarized in recent publications (Ishay *et al.*, 1991, 1992, 1993). One of the questions remaining unanswered, however, was whether the pupal silk responds to changes in temperature and if so, in what way. This question formed the linch pin of the present study in which, for comparative purposes, cocoons of the silkworm *Bombyx mori* were also measured.

MATERIALS AND METHODS

Silk caps from the cocoons of workers of the Oriental hornet were obtained from combs collected in fields in the environs of Tel-Aviv in the summer season of 1993. The removed caps were kept in sealed containers at room temperature until use.

Preparation for electrical measurement entailed hooking the cap to two copper electrodes of identical length; one affixed to the exterior and the other to the inner surface of the silk cap. The linkages were made via colloidal silver paint (Ted Pella, U.S.A.). The preparation was then measured for its electrical properties, mainly for current. The measurement was made through use of a Keithly 617 Programmable Electrometer (Cleveland, OH, U.S.A.) which received the measured data. Using its General Purpose Interface Bus (GPIB) (IEEE-488) capabilities it was connected to a PC, which served for monitoring and data logging. In order to obviate undesired influences of light or of electric and magnetic fields, the preparations to be measured were placed in a Faraday cage which in turn was placed in a Revco incubator model Pb-G-74, 5 V (Asheville, NC, U.S.A.). In this incubator it is possible to retain the desired conditions of humidity, illumination and temperature, which were the following: (a) a relative humidity (RH) of 90%; (b) maintenance in darkness; and (c) exposure of the various preparations to different temperatures. Regarding the temperature range, measurements commenced at a temperature of 5°C on

FIGURE 2 (*opposite*). The thermoelectric effect. The influence of heating on the current levels as measured on silk caps of pupae of the Oriental hornet. Six samples of current measurement are presented (a)–(f), each of them on a different cap. Curve b (in each sample) represents the control measurements, i.e. the whole measurement was performed at a low temperature of 5–8°C; curve a represents the test measurement in which after 40 min of measuring the sample at 5°C the temperature was gradually elevated up to 33–34°C. The changes in current followed accordingly. As can be seen in all the samples presented here (as well as in all others measured) the maximal current values were reached at 28–31°C which happens to be the optimal nest temperature. At higher temperatures the current levels decline. Ordinate: $4.000E-8 = 4.0 \times 10^{-8}$ A, $1.200E-7 = 1.2 \times 10^{-7}$ A.

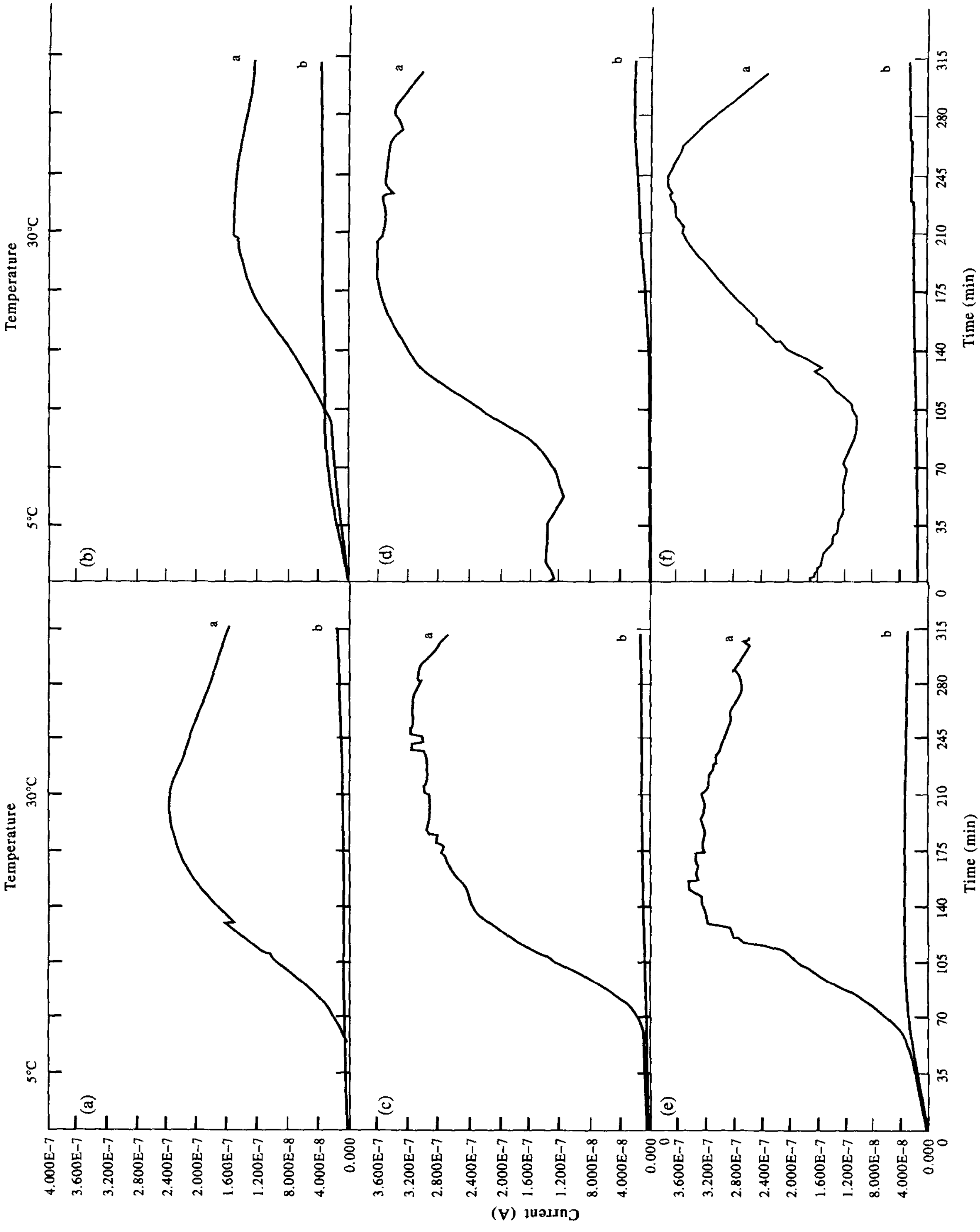

FIGURE 2 *Legend opposite.*

preparations introduced following overnight exposure to refrigeration at 4–5°C. The introduced preparations were maintained at this starting temperature (5°C) for about 30 min, followed by a gradual increase in temperature to a maximum of 33°C. Owing to incubator limitations, the rate of heating was not uniform, so that between 5 and 25°C the incubator heated more rapidly than it did between 25 and 33°C. Since the measurements were made under conditions of maximal RH for this type of incubator, it was not possible to reach a higher temperature than 33–34°C. As control for each measurement, each tested preparation was measured also at a low temperature of 5–8°C. Measurements were undertaken on both natural, intact preparations of silk caps collected from the combs as well as on preparations whose silk cap was first boiled for 5 min in tap water. Boiling was done and in order to ascertain whether the treatment possibly precipitates or "peels off" proteins present in the outer envelope of silk fibres.

Further details on the manner of preparing the silk caps can be found in previous publications (Morgan and Board, 1983). In total, 33 specimens were measured, 6 of them previously "boiled". Six cocoons of the silkworm *Bombyx mori* were prepared and measured in identical fashion.

RESULTS

Response of the silk caps to boosting of the ambient temperature is stereotypic (see Fig. 2) as follows. Immediately upon commencement of measurement, on a preparation that was pre-exposed to 4–5°C, the spontaneous current in it starts to rise moderately upon its placement in the incubator at the same temperature. The current values range between one and several dozen nAmp. This initial measurement, which lasts 30–40 min, constitutes a control to the subsequent measurements. With an increase in the temperature, one notices a sharp change in the rate of current increase which, in graphic terms, means that there is significant change in the slope of the curve. This change is visible in each of the curves given in frames (a)–(f) of Fig. 2. In the curve designated as "a" (with individual differences between each of the measured silk caps) the current reaches a maximum at a temperature of 28–31°C and then commences to drop gradually upon further increase in temperature. This phenomenon of changes in the strength of the current upon changes in temperature recurs many times with the same preparation on repeated measurements, following a period of relaxation in the cold which lasts at least several hours. In addition to the pre-heating control measurement, each preparation was measured also for its current values at low temperatures (5–8°C) without any further increase in temperature. The result of this second control measurement is given in plot "b" of each of the graphs (a)–(f). The maximal values obtained in these control measurements were found at the end of measurement, which were only slightly higher than those obtained in the first half-hour of test measurements, that is, prior to temperature hiking. In any event, the control measurements revealed no deviation from the slope of the test curve. In general, in all the measured preparations, the values obtained at a temperature of 28–31°C were, usually, higher by one order of magnitude than the control measurements for the same preparation. The response of silk caps that had undergone boiling was not different from those of unboiled silk caps, that is, the curve obtained from measuring boiled caps was similar to that with unboiled ones.

The results obtained by measuring cocoons of the silkworm *Bombyx mori* were similar in nature, albeit lower by one order of magnitude.

DISCUSSION

Our findings indicate that a single silk cap can gauge its ambient temperature, because upon *changes of temperature*, it displays *change in the intensity of the current* which corresponds to changes in the level of thermic energy in its ambience. In this sense, the silk seems to behave like a material which is an organic *thermoelectric energy converter*. A similar phenomenon has previously been described from the cuticle of hornets (Shimony and Ishay, 1981). It is of interest to note that the measured changes occur within the range of biological temperatures, while the maximal currents are recorded at optimal nest temperature (Himmer, 1932; Ishay *et al.*, 1967; Kemper and Döhring, 1967; Ishay and Ruttner, 1971; Spradbery, 1973; Edwards, 1980; Heinrich, 1980; Brian, 1983; Matsuura and Yamane, 1990) which is around 29°C.

The question arises as to which of the known thermoelectric effects does the phenomenon described herein belong, bearing in mind that we are not measuring the temperature of a single silk strand, but rather the electrodes are connected via a silver paint conductor to *numerous* silk strands. At face value, there is a need to rule out a Seebeck effect inasmuch as the electrodes attached to the silk cap were exposed in the incubator to the same temperature. In other words, this is not the classic case where voltage is created owing to a temperature gradient between the two electrodes. Another thermoelectric effect is the Peltier effect in which there is a different heat flow between the two electrodes, relative to the electric current flowing through the system. The two mentioned phenomena owe their existence to a junction between two materials possessing different properties of electric or thermic conductance. This notwithstanding, we are still dealing here with a junction between two different materials. It is the silk fibre in the pupal cocoon that is comprised of an elastic protein called fibroin which is wrapped in a protein called sericin (Ochiai, 1960). Each such fibre is double-stranded, that is, comprised of two identical filaments (each of which, as mentioned, is composed of an inner fibroin core and an outer sericin coating). These proteins originate from the labial glands of the larvae.

Trophallaxis, termed by Wheeler (1928), is the food exchange process between adults and larvae. Shortly after the larvae stops feeding, instead of secreting a solution containing various sugars and amino acids (from the very same labial glands) for the adults in the trophallaxis process (Ishay and Ikan, 1968), they release a material that is probably only (or mostly) proteinaceous. This material, upon contact with air, polymerizes to form a double-stranded, twin-layered thread with which the larvae spin their cocoon. The diameter of individual fibres ranges between 5 and 10 μm (Ishay and Ganor, 1990). It is reasonable to assume that all along the silk fibre, in every cocoon, in the junction between the envelope and the core, a local potential gradient is formed. Moreover, the silk is treated with several elements some of which are semiconductors, some of them electron donors and others electron acceptors (like titanium, vanadium, chromium, iron, copper and zinc) (Ishay and Ganor, unpublished observations), which may contribute to the process. Size of the silk molecule here is unclear. If to judge by what is known from the silk worm *Bombyx mori*, the molecule of fibroin consists of a heavy (H) chain (350 kDa) and light (L) chain (25 kDa) which are linked by a disulphide bond (Mizuno, 1992).

Whatever the case, we are probably dealing with a large molecule and the material in the outer envelope, namely, the sericin is immiscible in water in hornets unlike in *Bombyx mori*. The origin of the measured thermoelectric effect is the motion of electrons or holes that carry the electrical current in a conductor, which in the present case, is a molecular conductor with the conduction along the entire length of the fibrous silk strand. We deem the double-stranded silk string to be a semiconductor with a p–n junction, in which one layer, probably the inner one, donates the excess electrons

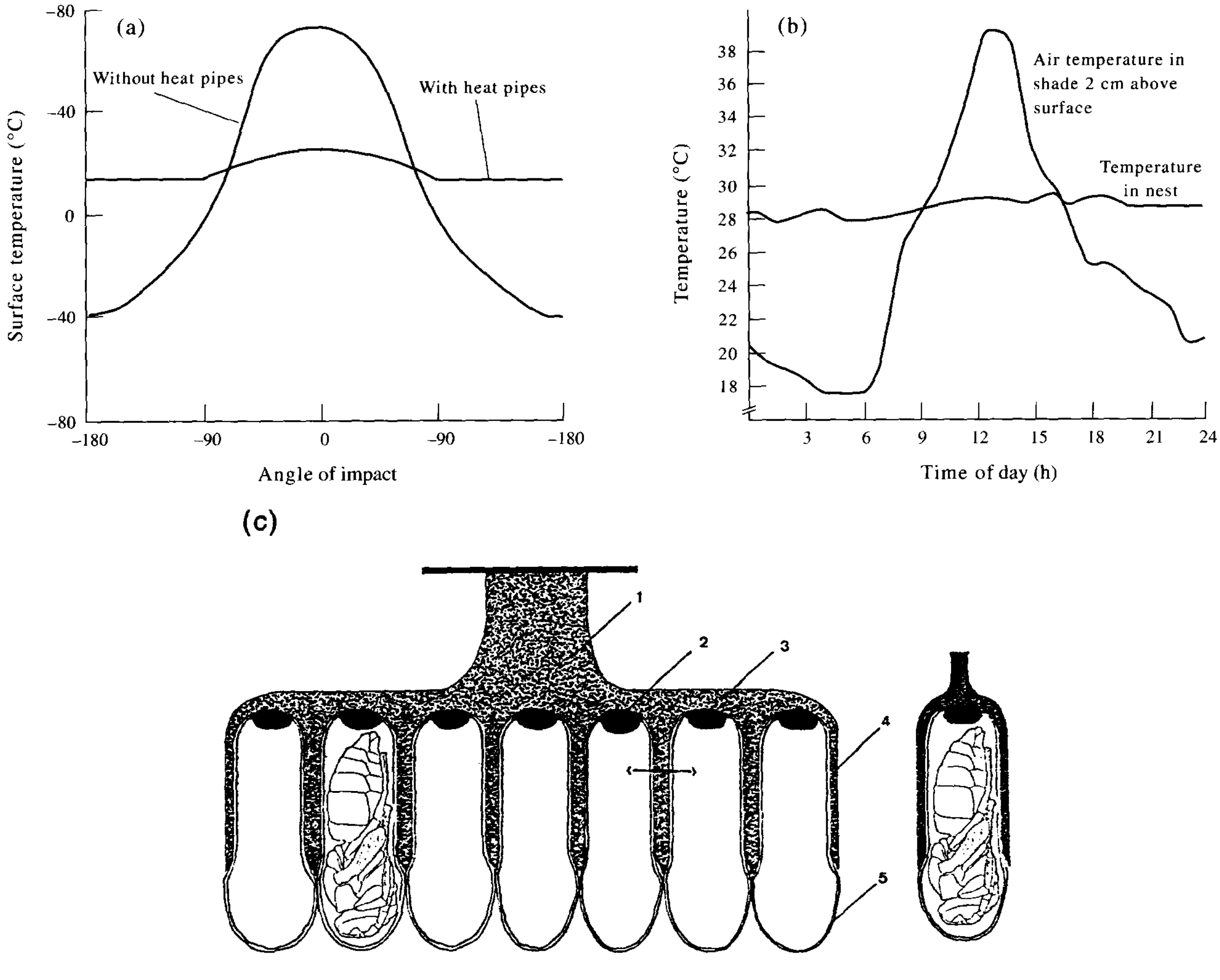

FIGURE 3. A comparison of the effect of heating pipes on temperature flattening in a satellite (courtesy Dornier Review) (a) and that of the Oriental hornet nest (b) (Courtesy Rentokill Limited): (a) abscissa the various angles of a satellite towards the sun's rays; (b) that of the exposure of the hornet nest towards the sun's rays during 24 h of the day. In both cases under the influence of the thermoregulator the temperature is kept inside narrow limits constantly; and (c) a schematic representation of a hornet comb. 1 = the stalk, 2 = meconium, 3 = the cell roof, 4 = the cell wall, 5 = the silk cap. Note that the normal comb position is vertical. If to describe the various details in terms of a classical heating pipe then 5 is the heat source, 4 = the adiabatic section, 3, 2, and 1 = the heat sink. The pupa inside the puparium is presented in the separate cell, and inside one cell of the schematic comb, in its right position.

(n-type) while the other (probably the external one) accepts them (p-type) or, alternatively the current is created at the border, i.e. at the junction between the two (core and coat). With a rise in the temperature there is also a rise in the number of electrons (or holes) passing from the valence to the conduction band and consequently an increase in the measured current. For greater detail, consult Gutmann and Lyons (1981) and Gutmann *et al.* (1983). As opposed to metallic conductivity, the conductivity of semiconductors is strongly dependent on temperature. The increase in temperature up to about 28–31°C is optimal and constitutes probably one of the unique features of this pupal silk since, as said, this is the optimal nest temperature. At temperatures above optimal, scattering due to phonons and charged impurities occurs thereby resulting in a decline in electrical conductivity (Ibach and Lüth, 1991). Alternatively, at temperatures above optimal, traps form which absorb electrons and "incarcerate" them. The number of traps formed is constantly rising the further we exceed the optimal temperature and consequently, it would seem that owing to the excess heating, the immediate yield should drop and comprise a reserve store for times of need.

Can we conjecture as to what transpires in nature when the pupa is encased in its silk coating? It is known that the pupa needs to be kept at a fixed or nearly fixed temperature, i.e. it needs constant isothermalization. Observations have shown that this is what happens, for a while at least, when the adult population is removed from the nest (Ishay and Ruttner, 1971), and this is despite the fact that until 2 days before eclosion the hornet pupae lack any muscles whose activation could create heat. In fact, despite the surrounding temperature, which is hot at midday and in the afternoon and cooler at night, the measured temperature in a hornet or wasp nest is flat throughout (see Fig. 3a). Such temperature flattening is well-known in industry, being produced by the so-called heating pipes (Fig. 3b) (Zandi, 1971; Chi, 1976; Dunn and Reay, 1982; Reay, 1982). Most of the heat in the nest, which is "donated" to the pupae originates from the bottom. The heat source, in fact, is the space between two adjacent combs, which happens to be saturated with water vapour. The cells in the combs of hornets and wasps are constructed of organic material—mainly cellulose mixed with soil—(which absorbs water) and in the direction of the gravitational force (Ishay, 1975; Ishay and Sadeh, 1975). The pupa inside such a cell is likewise oriented with gravity, so that its head is directed downward to rest against the cocoon's silk cap which is hydrophobic. In line with the recent experimental findings, it would seem that as the heat in the nest increases, part of it is picked up by the silk, where it converts it to an electric charge which is stored. Concurrently, excess heat is removed by evaporating water, the RH in the nest being 90% and higher (Ishay *et al.*, 1967). This water "climbs" around the pupae in the cell walls and by evaporation, cools the roof of the cells. As the pupa cools, ventilation of the adults, which is highly synchronized (Sadeh *et al.*, 1977) inside and at the nest opening, slows down. At the same time, part of the electric charge in the cocoon is released as an electric current, which can now flow to the coldest part of the cocoon and in the process also releases heat, much the same as humans do in their home by way of an electric heater or a toaster. This phenomenon is called Joule heating.

Inasmuch as the resistance in the pupal silk is high (10^5–$10^6\Omega/cm^2$) (Ishay and Ben-Shalom, 1992), the release of the current is slow and protracted. Hence, an entire hornet comb with numerous pupal cells may be regarded as a vertically-oriented flat heating pipe. What characterizes these heating devices in industry is their high efficiency in heat transmission. They capitalize on two familiar principles in physics namely, vapour heat transfer, with the heat absorption taking place from the bottom which is—the heat source, and a "wick" that is saturated with a volatile fluid which is intended to return the condensed moisture from the heat sink downward, so as to complete the circuit (Zandi, 1971). So far as heating of hornet pupae is concerned, the lines of analogy with industrial devices are: (1) their vertical "posture" within the cell; and (2) moderate heating which originates from below, with the heated "working fluid No. 1" (hemolymph) ascending to the upper part of the pupal body, where it loses some of its heat. The haemolymph is constantly pumped downward by action of the pupal heart (which can be roughly regarded as a wick). This haemolymph is responsible for disseminating the heat in near isothermal fashion within the spaces inside the body.

The silk coating (and the air layer between the silk and the pupa) acts first as an insulator between the pupa and its environment, second as an energy accumulator which stores electric charge during periods when there is excess energy (in traps), and third as a releaser of heat via the conduction of electric current wherever there is need for heating. "Working fluid No. 2" is the water which is always ascending outside the cocoon; this water is vapourized and excess RH is removed by almost constant ventilation (Sadeh *et al.*, 1977) performed concurrently by many adults and thus representing a mutual effort to maintain an equilibrium, by cooling the area. In sum, then, we are led to the conjecture that possibly one of the reasons why the combs of Vespinae are constructed in strict orientation towards the gravitational force, could be to ameliorate the thermoregulation as afore-described. If this is true, then the entire apparatus associated with this thermoregulation could be assigned the status of *thermoelectric heating pipes*. The development of this rather sophisticated thermoregulatory device can be regarded as a breakthrough that has enabled the Vespinae arising from the tropics (Wilson, 1971) to penetrate, spread and succeed during the warm season of the year in the subtropics and temperate zones of the world.

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