Natural Thermoelectric Heat Pump in Social Wasps

Jacob S. Ishay,[1,*] Vitaly Pertsis,[1] Eran Rave,[2,†] Alon Goren,[3,‡] and David J. Bergman[2,§]

[1]*Department of Physiology and Pharmacology, Sackler Faculty of Medicine, Tel Aviv University, Tel Aviv 69978, Israel*
[2]*School of Physics and Astronomy, Raymond and Beverly Sackler Faculty of Exact Sciences, Tel Aviv University, Tel Aviv, 69978, Israel*
[3]*Biomedical Engineering Department, Faculty of Engineering, Tel Aviv University, Tel Aviv 69978, Israel*

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Photographs of wasps or hornets, taken with different temperature sensitive infrared cameras, reveal body temperatures that are sometimes significantly lower than the ambient temperature. This suggests that the hornets possess an intrinsic biological heat pump mechanism which can be used to achieve such cooling. Evidence is presented to substantiate this novel suggestion and to argue that the heat pump is most likely implemented by exploiting a thermoelectric effect in the hornet cuticle. Such a natural heat pump can conceivably also serve to cool the active hornet, engaged in daytime activities outside the nest at ambient temperatures exceeding 40 °C, to a body temperature that is low enough to allow its survival in extreme thermal conditions. It might also function as a means of raising the body temperature up to a level that enables the hornet to remain active even when the ambient temperature is as low as 10 °C.

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Social hornets and wasps of the subfamily Vespinae (Hymenoptera) are common both in the Northern and Southern Hemispheres [1]. They reside in nests that are usually dug in the ground by the worker hornets, who also furnish them with constructed combs similar in shape to those found in a beehive. Each comb consists of a fairly regular array of haxagonal cells, in which the queen hornet lays eggs that develop into new adult hornets while looked after by the worker hornets. The prevailing temperature in the nest is around 29 °C [2,3]. The worker hornets undertake foraging excursions outside the nest which last from 20 sec up to 30 min or more, and extend to distances ranging from a few meters up to a few kilometers [4,5]. In the course of these outings, the ambient temperature may range from about 20 °C up to as high as 60 °C or more. It is generally accepted that during this foraging activity heat is generated by the thoracic flight muscles of the hornet [6], and is transmitted to other parts of its body mainly by the flow of haemolymph. This mechanism by itself can only lead to a body temperature of the hornet that is higher than the ambient temperature.

We have been studying the local external body temperature of oriental hornets under different conditions, using temperature sensitive infrared (IR) cameras. Selected photographs, taken using two different cameras, are shown in Fig. 1: Panels (a), (b) show hornets in various stages of recovering after being anesthetized by ether vapor, on different occasions, using a different camera each time. Panel (c) shows a hornet returning to a fully functioning natural hornet nest maintained throughout the summer on a window sill of our laboratory. Panel (d) shows a hornet leaving that same nest. These photos show various types of temperature distributions over the outer cuticle of the hornet. The details of each of those distributions depend on the type of activity or state of the hornet in question. However, a striking characteristic of all the distributions shown is that a certain part of the cuticle exhibits a temperature that is well below the ambient temperature. In panel (a) the entire body is 2–3 °C colder than the surroundings, which consist of a natural comb from a hornet nest in the field. A similar photograph, appearing in panel (b), shows three of the hornets from the window sill nest, at the center and bottom right, with a body temperature that is lower than the surroundings by 1°, while the compound eyes of at least the central hornet are colder by yet another 1°, and the lower tip of its abdomen is in between those two temperatures. In panel (c) it is the entire abdomen that is cooler by 2.5 °C, as compared to the surroundings which are mostly the plywood exterior of the box housing the window sill hornet nest, while the thorax is warmer than those surroundings by 4.5 °C. In panel (d) it is evident that the wings of the hornet are cold.

In order to test for possible effects of emissivity contrast on the apparent temperature, we also took photographs of dead hornets, using the same camera and the same backgrounds/surroundings as in panels (b)–(d). These control photos show that the emissivity contrast can be responsible for an apparent temperature lowering of the cuticle by no more than 0.9 °C.

That the live hornet can be hotter than its surroundings is no surprise: Its natural metabolism can easily account for that. By contrast, cooling part or all of its body to a lower than ambient temperature can only be achieved in two ways: (a) evaporation, (b) pumping heat. Although evaporation (of sweat) is used by most mammals to cool their bodies, insects are distinguished by having an external shell that is usually dry: The cuticle has no sweat glands for secretion of moisture. Also, the channels that traverse its thickness do not reach all the way to the

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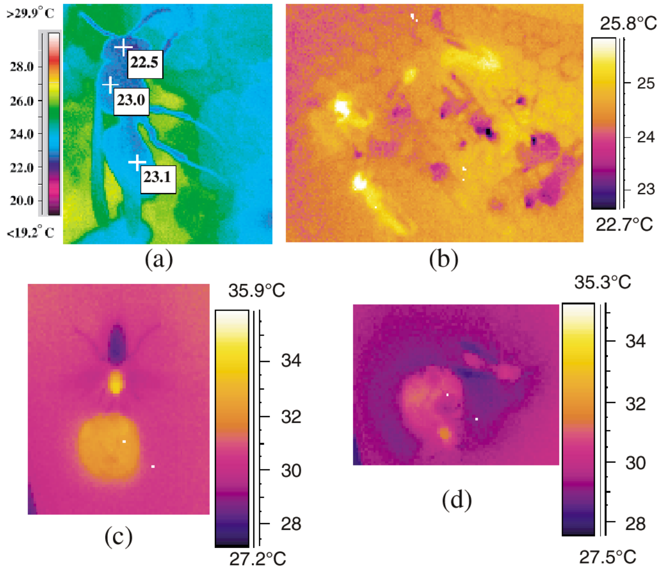

FIG. 1 (color). Photographs of hornets taken with infrared cameras capable of temperature discrimination. The image in (a) was taken in summer 1998 using a Thermacom Model 290 PM camera and processed by commercial Thermonitor 95 software, both from Inframetrics USA. The images in (b)–(d) were recorded in October–November 2002 using a FLIR ThermaCam SC500 (7.5–13 μm) and a PC card interface Agema THV550, and were analyzed by software application ThermaCam Researcher version 2001. (a) Hornet anesthetized in its natural nest at night by ether vapor, lying on comb before recovery. (b) Similarly anesthetized hornets, at daytime in the laboratory, lying on comb during recovery stage. In (a), the color coded temperature and exhibited spot measurements of body temperature reveal that the outer shell of the hornet is as much as 3 °C cooler than the comb. In (b) one can discern six hornets in the recovery stage from ether vapor anesthesia. A hornet slightly to the right of center and two others at the lower right side are cooler than the comb. All three exhibit coldest temperatures in small isolated regions or spots. In the case of the hornet near the center, one such cold spot is located at the tip of the abdomen and an even colder spot is located at or near the compound eyes. The latter cold spot is 3° C cooler than the comb. Above this hornet, another one can be discerned whose wings are cool though its body is warm, compared to the comb. More to the left are two more hornets with warm bodies, and even warmer heads: The head temperatures are up to 2 °C warmer than the nearby comb, and 4 °C warmer than the cold eyes of the central hornet. (c), (d) Routine activity near the entrance to a natural hornet nest which the wasps built and maintained during an entire active season (May through October 2002) in a plywood box positioned on a laboratory window sill. The entrance can be discerned as a circular hole of diameter 2.5 cm in the box wall at the bottom, where the apparent temperature is somewhat higher than the exterior surface of the wall. In (c) a hornet is seen walking on the exterior of the wall just before it enters the nest, after having flown in several seconds earlier from an outing. In (d) a hornet is seen who has just exited from the nest, and is about to take off on a foraging flight. In this case, both the thorax and the abdomen are apparently somewhat warmer than the surroundings, though not warmer than the nest interior, but the wings are cooler, by about 1 °C, than the plywood outer nest wall.

external surface. They do not extend through the external coating of wax and cement [7], therefore there is no possibility to have moisture released from the inner body so as to wet the external shell. The only places where such moisture secretion is possible, and was sometimes observed by us, is from the mouth and sting of the hornet. We are thus lead to the inescapable deduction that the hornet must employ some kind of heat pump in order to eject body heat to the surroundings even when those are warmer than its body.

This heat pump needs to operate in the cuticle itself: Otherwise it would be very difficult to cool the entire outer body area below ambient, or to cool the wings, over most of which there is almost nothing besides two layers of cuticle [7].

How such a heat pump might work becomes an intriguing question which we now address: The simplest types of heat pump operate between thermal reservoirs at two different temperatures, and they use work in order to transfer heat from the lower to the higher temperature. This work can be either mechanical, as in the case of the conventional household refrigerator or air conditioner where a mechanical compressor is used, or electrical, as in the case of a thermoelectric heat pump [8]. The need to invest work in order to pump heat can be avoided in the case of a heat pump operating with three thermal reservoirs, as in the case of the domestic gas refrigerator which uses a sorption/desorption cycle [8]. In this case, heat is absorbed from both the lowest and the highest temperature reservoirs and is ejected to the intermediate temperature reservoir. The hornet at night, or even in a daytime shade without direct exposure to the sun, has at its disposal only two thermal reservoirs: Its body and its surroundings. Therefore its heat pump needs work for its operation. Since there is no possibility of doing mechanical work in the cuticle, we are forced to conclude that the cuticle heat pump must use electrical work, i.e., it is a *thermoelectric heat pump*. The electric power for operating this heat pump can be produced by an electrochemical reaction in the hornet body. Additional electric power could perhaps be produced by a photovoltaic effect in the cuticle when it is irradiated by sunlight [9–13].

It should be noted that the natural cuticle heat pump does not need to operate continuously. In fact, while it is operating, the outer shell of the hornet has to be warmer than the neighboring outside air in order for the pumped heat to be ejected. However, intermittent operation of the heat pump can result in a body temperature, both internal and external, that is lower than ambient. In the case of the outer shell temperature, that would be lower than ambient only during the “quiescent periods” in between two adjacent “active periods” of heat pumping. Indeed, in Fig. 1(b) we see that, although the three recovering hornets mentioned earlier have outer shells which are cooler than ambient, another three recovering hornets (at the top and left) have outer shells which are warmer than ambient. In conclusion, intermittent operation of a natural thermoelectric heat pump in the hornet cuticle is how we envision that it manages to cool its body, including the outer shell, to temperatures below ambient. In future studies, we will try to verify the hypothesized intermittency of heat pump operation by direct observations.

Besides requiring an appropriate source of electric power, in order to operate an effective heat pump the hornet also needs for its cuticle to have appropriate values of some crucial material parameters: These are the electrical conductivity σ, thermal conductivity κ, and thermopower or Seebeck coefficient S. In particular, the maximal lowering of temperature $\Delta T_{\max} \equiv T_H - T_C$ attainable by a "one step" heat pump made of one such thermoelectric material is given by [14]

$$\frac{\Delta T_{\max}}{T_C} = \frac{1}{2} Z T_C, \qquad Z \equiv \frac{\sigma S^2}{\kappa},$$

where Z is the "thermoelectric figure of merit." Although the dimensionless positive material parameter ZT is, in principle, unbounded, in practice most materials have ZT values between 0.01 and 0.001 [15]. By contrast, the high quality thermoelectric semimetal $\mathrm{Bi_2Te_3}$ has $ZT \cong 0.6$ at room temperature [15]. Although some measurements of σ and S in the hornet cuticle have been published [16], those were invariably made along directions parallel to the cuticle. No measurements of κ were ever made. Using the values $\sigma = 0.16\ S/\mathrm{m}$ and $S = 0.002\ \mathrm{V/deg}$, which are deduced from Ref. [16], and $\kappa = 0.1\ \mathrm{J/(s\,m\,deg)}$, a value typical of wood, we get $ZT = 0.002$. This leads to $\Delta T_{\max} \cong 0.3^\circ\ \mathrm{C}$ when $T_C = 300\ \mathrm{K}$. This is about a factor 10 smaller than some of the coolings reported above. Clearly, it is now important to measure all the material coefficients σ, S, κ of the hornet cuticle in a reliable fashion in the direction perpendicular to the cuticle surface. That will allow us to decide whether the thermoelectric heat pump is capable of producing the cooling effects which were observed. In this connection, it is important to note that the cuticle has an extremely anisotropic microstructure—see the electron micrographs of cuticle sections in Figs. 2(a)–2(c). Therefore we can expect that the physical properties in the direction perpendicular to the surface will be quite different from those in the parallel directions.

It should be pointed out that the heat pump will not only have to maintain a fixed temperature differential of the hornet with respect to its surroundings, but also to dispose of the metabolic heat that is produced by the insect even when it is resting.

Additional support for the proposition that hornets deploy a natural thermoelectric heat pump comes from the following observations:

(a) As shown in Ref. [13], vespine cuticle exhibits a photovoltaic effect characteristic of semiconductor p-n junctions when exposed to visible or ultraviolet (UV) light. The resultant photoinduced voltage was measured along the cuticle surfaces and was found to have opposite signs on the inner and outer surfaces.

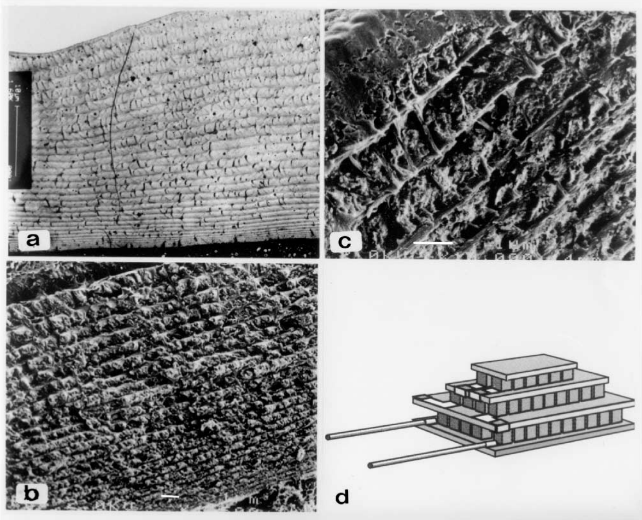

FIG. 2. (a) Transmission electron micrograph (TEM) [17] of a section of hornet cuticle. The size scale is indicated by a vertical bar at the left which represents 10 μm. At the top there appears a 0.2–0.3 μm thick epicuticular layer, and beneath it a 1 μm thick exocuticular layer. Proceeding toward the interior, these two layers are then followed by about 30 more roughly parallel endocuticular layers of decreasing thickness. The bottom layers, which are barely discernible, are about 10 times thinner than the exocuticular layer. (b) and (c) show scanning electron micrographs (SEM) of similar sections, at different magnifications, as denoted by the horizontal scale bars at the bottom which represent 1 μm. (b) shows an entire cross section, comprising about 25 layers, similar to the section described in (a). (c) shows only about 10 layers of a similar section but at higher magnification. In the preparation process of the latter sample, part of the contents of individual layers was lost by material leakage, leaving mainly the skeleton of each layer. Consequently, the intralayer microstructure is more clearly visible in (c) than in (a) and (b). Note that, apart from the flat laminar structure of the nearly parallel layers, each layer seems to be additionally divided into cells which are separated by walls that are approximately perpendicular to the layer. (d) Picture of a commercial multistage thermoelectric heat pump device (Marlowe Industries Inc., Dallas, TX), whose linear dimensions, albeit variable, usually amount to a few centimeters. Note the superficial similarity in microstructure of this device and the cuticle sections displayed in (a)–(c), especially the one in (c), even though the size scale differs by a factor of 10^4.

(b) Wasps need to lower their body temperature by several degrees also when they are active outside the nest in daytime, where the ambient temperature can be as high as 40–60 °C. Such daytime cooling is more difficult than nighttime cooling or daytime cooling in the shade, when the hornets are "inactive" and therefore produce less metabolic heat. However, exposure to the flux of visible and UV sunlight induces electric voltages and currents in the cuticle, as described in Ref. [13], and these could provide an additional source of electric power for driving the thermoelectric heat pump.

(c) The hornet cuticle has a microstructure that is strikingly reminiscent of the microstructure used in fabrication of practical commercial thermoelectric heat pumps, albeit the size scale is quite different. This is best appreciated by viewing SEM and TEM pictures of cuticle sections at various magnifications [see Figs. 2(a)–2(c)] alongside a picture of a commercial multilayered thermoelectric heat pump approximately 5 cm long [see Fig. 2(d)]. In this regard, it is also significant that a laminar composite material, made of parallel layers of a good metal and a high quality thermoelectric material arranged perpendicular to the direction of the electric and thermal fluxes, has recently been shown to allow a maximal enhancement of the "thermoelectric power factor" while resulting in a minimal degradation of the "thermoelectric figure of merit" [18]. The cellular microstructure, which is apparent in each layer of the commercial heat pump, is designed to have alternating thermoelectric elements with p-type and n-type charge carriers that conduct electricity in series but conduct heat in parallel, with the different types of currents all flowing in a direction perpendicular to the layer. It is intriguing to speculate whether the layered cellular microstructure of the cuticle is related to similar functional design concepts.

As far as we know, this is the first instance where a natural biological heat pump has been proposed to function in a living creature. It is also the first time that a thermoelectric effect is deemed to play a role in the physiology of any living creature.

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*Electronic address: physio7@post.tau.ac.il
†Electronic address: eranr@post.tau.ac.il
‡Electronic address: aloncoh@post.tau.ac.il
§Electronic address: bergman@post.tau.ac.il

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