Thermoregulation in Bees

Bees regulate their body temperature by means of behavior, morphology and physiology, which helps them to meet individual and social needs

Bernd Heinrich and Harald Esch

Otto Plath, a Harvard entomologist and father of the poet Sylvia Plath, once summarized the common wisdom about how bees respond to changes in temperature. "Like all cold-blooded animals," he wrote, "honeybees and bumblebees have no means of regulating their body temperature, and their exposure to cold invariably results in lethargy, and often death."

Many have shared the belief of Plath, who wrote more than half a century ago, that insects are poikilotherms, animals that cannot regulate their body temperature. Nevertheless, thermoregulatory behavior is particularly well developed in several insects and particularly in bees, which can adjust their body temperature over a wide range of environmental conditions. Bees need thermoregulation to fly, to forage and to incubate their young. The mechanisms they have developed to accomplish these tasks are as diverse as bees themselves.

Bees are a diverse group of insects in both social organization and environmental range. Some are strictly solitary; others are highly social, having tens of thousands of individuals in a colony. In addition, different species can be found across an extraordinary range of the earth's thermal environments. Bees are at home in hot deserts and lowland tropical jungles along the equator, and two species can be found in the High Arctic, within 82 kilometers of the North Pole.

It has been known for more than 250 years that bees have colony-level thermoregulation. This response determines where the animals can survive winter. Individual thermoregulation by bees, however, was discovered relatively recently. It is ecologically important because it determines when and where a bee can fly and forage.

Technical difficulties have long hampered progress in deciphering the physiological mechanisms of how insects as small as bees can regulate their body temperature at levels close to that of human beings. In recent years, however, the combined work of our laboratories and several others has provided a wealth of data that are producing a coherent picture of the diverse thermoregulatory mechanisms of individual bees. Much of the research has concentrated on bumblebees, carpenter bees and honeybees, because these animals encounter unique thermal problems. Although the immediate objective has been studying the extremes of adaptation, we shall show that the end result is a general understanding of how the thermal environment has shaped bees as we see them today.

No-Shake Shivers

Almost no insects, except possibly some social bees, maintain a continuously high body temperature. Instead, an insect remains cool—its body temperature near the ambient temperature—until it prepares for flight, at which time it "warms up," increasing its body temperature to at least 30 degrees Celsius, and sometimes over 40 degrees Celsius. The process can be surprisingly rapid. A bumblebee, for example, can warm up from an air and body temperature of 13 degrees Celsius to 37 degrees in just six minutes. In all insects that warm up by producing their own heat (some do so by basking in sunshine), the increased body temperature is restricted largely to the thorax, the mid-portion of the body that is packed with flight muscles.

The wings of some insects, such as moths, vibrate during warm-up, but bees warm up silently, with no thoracic vibrations or wing movements. Nevertheless, working with Ann Kammer of Arizona State University, one of us (Heinrich) showed that warm-up in bees always includes activation of the thoracic flight muscles: the dorsal longitudinal muscles, which depress the wings, and the dorso-ventral muscles, which elevate the wings. The problem of how bees generate heat without vibrating, however, remained unsolved.

Warm-up in bees depends on the physiology of their flight muscles, which are called fibrillar or myogenic. A conventional muscle, such as the ones that move the human skeletal system, contracts only after receiving an action potential, or an electrical impulse from the nervous system. A fibrillar muscle, on the other hand, contracts when it receives an action potential or when it is stretched within a few hundred milliseconds after receiving an action potential; hence it is also called a stretch-activated muscle.

During flight, the activation of a bee's wing muscles results from both stretching and nervous input. The contraction of the downstroke muscles depresses the wing and, at the same time, stretches the upstroke muscles, which then contract and lift the wing, stretching the downstroke muscles and so on. The central nervous system sends occasional action potentials to the flight muscles to "spark" the cycles of contraction. This system generates oscillations of the upstroke and downstroke muscles at higher frequencies and with

---

Bernd Heinrich is professor of zoology at the University of Vermont. He earned his Ph.D. in 1970 from the University of California at Los Angeles. He has written five books, the most recent of which is The Hot-Blooded Insects. *Harald Esch is professor of biological science at the University of Notre Dame. He earned his Ph.D. in 1960 from the University of Wuerzburg. He has published research on communication, flight behavior and thermoregulation in bees and other insects. Address for Heinrich: Department of Zoology, Marsh Life Science Building, the University of Vermont, Burlington, VT 05405–0086.*

Figure 1. Flying honeybee must regulate its body temperature. Although insects are usually considered cold-blooded, many bees exhibit thermoregulation, allowing them to fly in cold and warm temperatures and to inhabit different environments. Many species of bees stay warm in cold temperatures and cool in hot temperatures through behavioral, morphological and physiological adaptations.

better precision than neuronal input alone could generate. Bumblebees, for instance, beat their wings about 200 times each second during flight.

If a myogenic muscle is removed from a bee's thorax, it behaves like a conventional muscle, contracting only when it receives an action potential. The isolated muscle produces more tension if the frequency of action potentials increases, but the tension reaches a peak, called tetanus, at an action-potential frequency of 15 times per second.

During warm-up, the flight muscles behave like isolated muscles, contracting in response to action potentials. Kammer and Heinrich found that a bumblebee's flight muscles receive up to 40 action potentials per second during warm-up, which contracts the muscles in a relatively tight tetanus. These tetanic contractions produce considerable tension, but little motion, which explains the lack of wing vibrations. These results, however, do not explain how a bee's flight muscles are used differently during warm-up and flight.

One of us (Esch) answered this question in collaboration with Franz Goller. Esch and Goller monitored simultaneously the action potentials to the flight muscles, the thoracic and ambient temperatures and the movement of the scutellum, a piece of cuticle at the top rear portion of the thorax. Through anatomical inspection, Esch and Goller reasoned that a contraction of the dorsal longitudinal (or downstroke) muscles should rotate the scutellum until the scutellar arms (downward projections of the scutellum) hit a projection at the rear of the thorax, thereby creating a mechanical stop that prevents stretch activation of the flight muscles.

Esch, Goller and Heinrich examined bumblebees, carpenter bees and honeybees as the animals alternated between bouts of warm-up, occasional buzzing, flight and rest. The beginning of flight-muscle action potentials was always associated with scutellar movement and increases in thoracic temperature. Moreover, there was never an increase in thoracic temperature without action potentials, and all action potentials induced muscle contraction as determined by scutellar movement. The activation of a dorsal longitudinal muscle moved the posterior part of the scutellum downward, and a dorsoventral muscle moved it upward.

The key to keeping the flight muscles motionless during warm-up depends in large part on the ratio of activation of the two sets of flight muscles. Although both sets of muscles are activated essentially si-

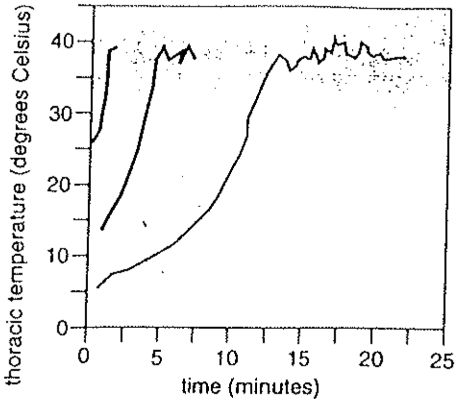


Figure 2. Bee warms up by contracting its flight muscles. A bumblebee in an ambient temperature of 24 *(blue)*, 13 *(red)* or 7 *(yellow)* degrees Celsius can quickly increase its thoracic temperature to a flight-ready level near 40 degrees. Warm-up may take several minutes in cold temperatures.

multaneously during warm-up, the dorsal longitudinal muscles are activated more frequently, especially in bumblebees and honeybees. This imbalance rotates the scutellum until it is stopped mechanically. These results indicate that the dorsal longitudinal muscles stretch the dorso-ventral muscles until the scutellum hits its mechanical stop. That prevents the muscles from being stretch-activated, and no oscillatory contractions develop. Flight oscillations begin with a burst of action potentials to the dorso-ventral muscles, which pulls the scutellar arms from the mechanical stop and initiates the alternating contractions. When the dorsal longitudinal and dorso-ventral muscles contract alternately, the scutellum is never depressed enough to hit its mechanical stop, allowing stretch activation.

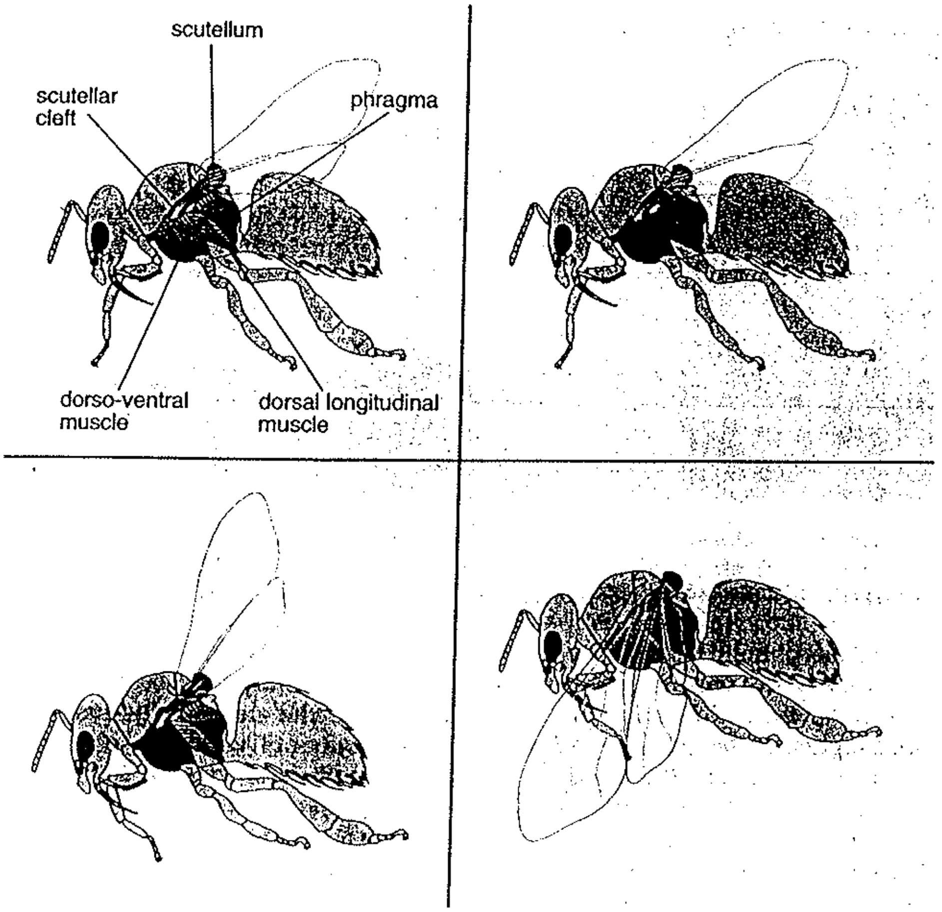


Figure 3. Warm-up proceeds without visible movement in some bees. The process involves the flight muscles *(pink)*—the dorsal longitudinal and dorso-ventral muscles, which move the wings indirectly through levers—and the scutellum (the rear portion of the thorax, which projects downward as the scutellar arms). The dorso-ventral muscles extend from the top to the bottom of the thorax; the dorsal longitudinal muscles extend from the top of the thorax to a freely moving structure called the phragma, which pushes the scutellar arm. Before warm-up *(top left)*, the flight muscles are relaxed, leaving an opening, called the scutellar cleft, between a scutellar arm and the front portion of the thorax. During warm-up *(top right)*, both sets of flight muscles contract simultaneously *(red)*, but the dorsal longitudinal muscles contract more. This imbalance of contraction rotates the scutellar arms into the thorax, creating a mechanical stop that prevents further movement, thereby generating motionless warm-up. Flight begins with a contractile burst to the dorso-ventral muscles, which rotates the scutellar arms away from the mechanical stop and raises the wings *(bottom left)*. The dorsal longitudinal muscles then contract, depressing the wings *(bottom right)*. The upstroke muscles contract again before the scutellar arms hit the mechanical stop.

In carpenter bees, the dorso-ventral muscles are activated more than the dorsal longitudinal muscles. This prevents mechanical fixation of the scutellum, and these bees show some movement of the thorax during warm-up. These movements do not lead to oscillations because the balance of forces between the two sets of muscles is upset, and this alone is enough to prevent oscillations. Carpenter bees switch from warm-up to flight when a burst of action potentials is sent to the dorsal longitudinal muscles.

The ability to "shiver" gives bees numerous options. They can save energy by remaining in torpor and allowing their body temperature to remain low. When flowers bloom, the bees warm up and fly. Shivering, however, also allows bees to maintain a continuously high and stable body temperature during foraging, so they can move quickly from one flower to another.

Heart Loops and Honey Drops

Differences in thermoregulation among honeybees, bumblebees and carpenter bees emerge largely because they occupy different habitats. The honeybee is of tropical origin, but it has been able to invade the northern temperate zone because of its social organization—warmth generated from the many individuals in a hive—and its habit of nesting in tree cavities. Foragers in the field, however, must face the thermal challenges alone, demanding adequate morphological and physiological designs. A crucial feature of a honeybee's thermoregulation arises from its circulatory system, which helps retain heat in the thorax.

In insects, heat is lost directly from the thorax to the air, and usually also through the abdomen. A bee's abdomen, which contains the honey stomach, can weigh four times as much as the thorax, and the abdomen could draw most of the heat out of the thorax. Only the thorax, however, must remain hot for the insect to be flight-ready. If a bee could shut off all unnecessary heat loss to the abdomen, it could forage at lower ambient temperatures.

Honeybees have a short thoracic pile, composed of hairs, that retards convective heat loss from the thorax, but a more important mechanism is a counter-current heat exchanger. It eliminates almost all heat loss to the abdomen, despite the fact that blood must transport fuel from the abdominal honey-stomach to the thoracic flight motor.

A honeybee's heart is located in its abdomen. The heart pumps blood from the abdomen into the head through the aorta. The blood returns to the heart through the open body cavity. A honeybee's aorta is arranged in nine loops in the narrow petiole area, or waist, that connects the abdomen to the thorax. The blood is heated in the thorax and then flows back around these loops before returning to the abdomen. The loops promote counter-current heat exchange in three ways. First, they create a large surface for heat exchange, so that heat from the warm blood flows into the cooler petiole, where the heat is returned to the thorax. Second, resistance in the loops slows the blood, allowing more time for heat exchange. Third, the loops obliterate discrete pulses of blood that might otherwise be shuttled quickly through the petiole without heat exchange. In support of the heat-exchanger hypothesis, we and other investigators find that honeybees never heat up their abdomens, even when the thorax is heated to near-lethal temperatures.

In addition to flying at low temperatures, honeybees can fly at higher temperatures than any other insect of their size. A flying honeybee generates a temperature excess of about 15 degrees Celsius over a broad range of ambient temperatures, from 17 to 25 degrees. Heinrich found that honeybees can fly at the extraordinarily high air temperature of 46 degrees Celsius, and that when doing so they maintain an astonishing average thoracic temperature of only 45 degrees. Only evaporative cooling can decrease body temperature below the ambient temperature, and a honeybee dissipates enough heat to depress its thoracic temperature some 17 degrees below what it would be if only convection was available.

Esch observed long ago that a honeybee flying at high temperatures in a wind tunnel often extrudes a droplet of liquid on its tongue, and Heinrich later discovered that the droplet is a key to a honeybee's thermoregulation. If a tethered honeybee's head is heated, the bee regurgitates nectar from its honeycrop when its thoracic temperature reaches 46 degrees Celsius. Evaporative cooling from the liquid cools the head immediately, and the cooled head withdraws heat from the thorax, which is coupled to the head by blood circulation and close physical contact. Even placing a drop of fluid in a dead bee's mouth almost immediately reduces its thoracic temperature. In live bees, the heat loss exceeds that of passive cooling because high-amplitude aortic pulses probably increase the blo flow to the head.

Paul D. Cooper and William A. Sh fer of the University of Arizona o served regurgitated droplets of nect in honeybee nectar foragers when th returned to their hive from a h desert. Pollen foragers, however, d not display that behavior, probably b cause they do not forage at the hi temperatures that nectar foragers do

Nectar regurgitation is not unique honeybees. Other bees, including ho eybees, regurgitate nectar to conce trate it. Undoubtedly, the thermoreg latory function is derived from th honey-making function. As we hav shown, however, a honeybee's dropl of nectar serves two purposes: It re moves excess water from the nectar a part of the honey-making process, an it allows honeybees to gather mor nectar by foraging at temperatures tha ground most of their competitors wit heat prostration.

Bumble Beats

Perhaps the best-known thermoregu latory characteristic of bumblebees i their "fur coat." British biologist Norman S. Church showed 30 years ag that the fur coat approximately halve a bumblebee's rate of heat loss. Never

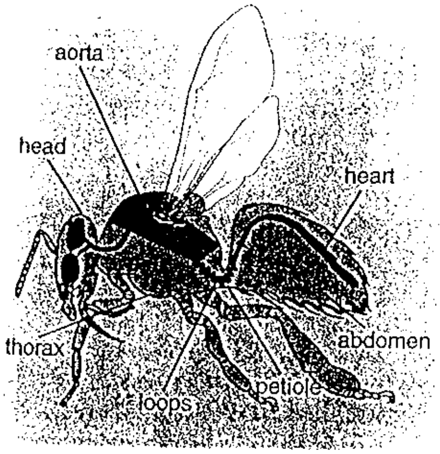


Figure 4. Honeybee's heart keeps heat in the thorax, which must stay warm for flight. Blood is pumped from the heart, located in the abdomen, through the aorta and into the head, where the blood empties into the body cavity. The blood in the body cavity moves through the thorax, where it is heated by the activity of the flight muscles *(pink)*, and then back to the abdomen. Body-cavity blood moving from the thorax to the abdomen passes through the petiole, where the heart forms nine loops. The cool blood in the loops absorbs heat from the warm body-cavity blood before it returns to the abdomen.

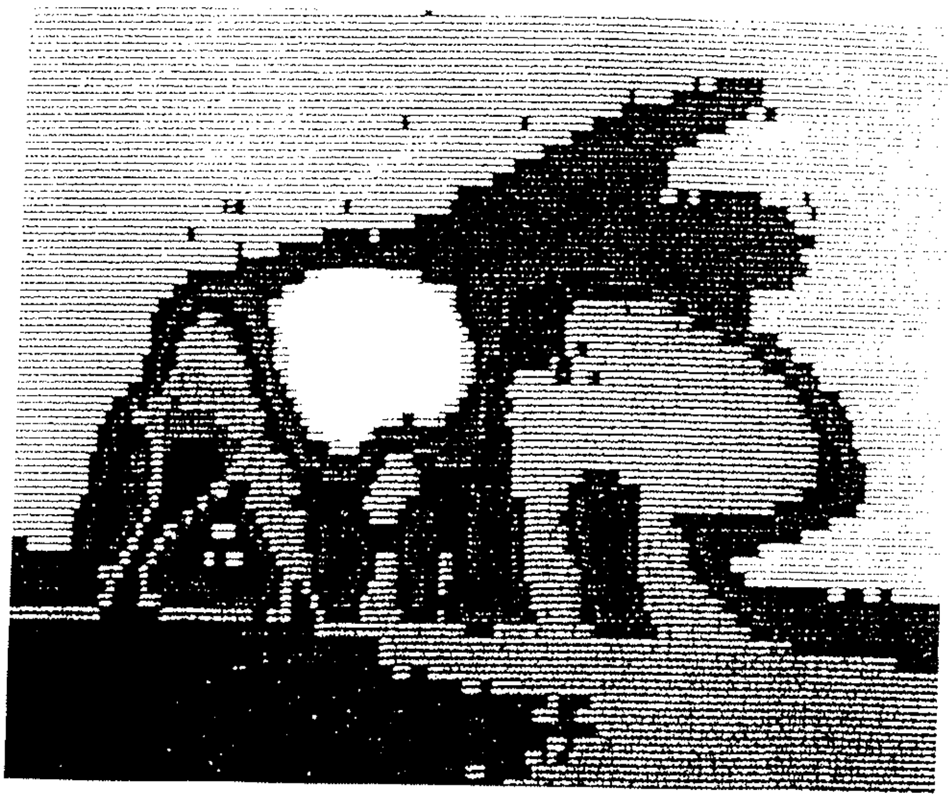


Figure 5. Heat trapped in the thorax is evident in an image showing temperature distribution in a honeybee. This honeybee's thorax is warm *(white)*, and its abdomen stays cool *(green)*. (Illustration courtesy of Sigurd Schmaranzer and Anton Stabentheiner.)

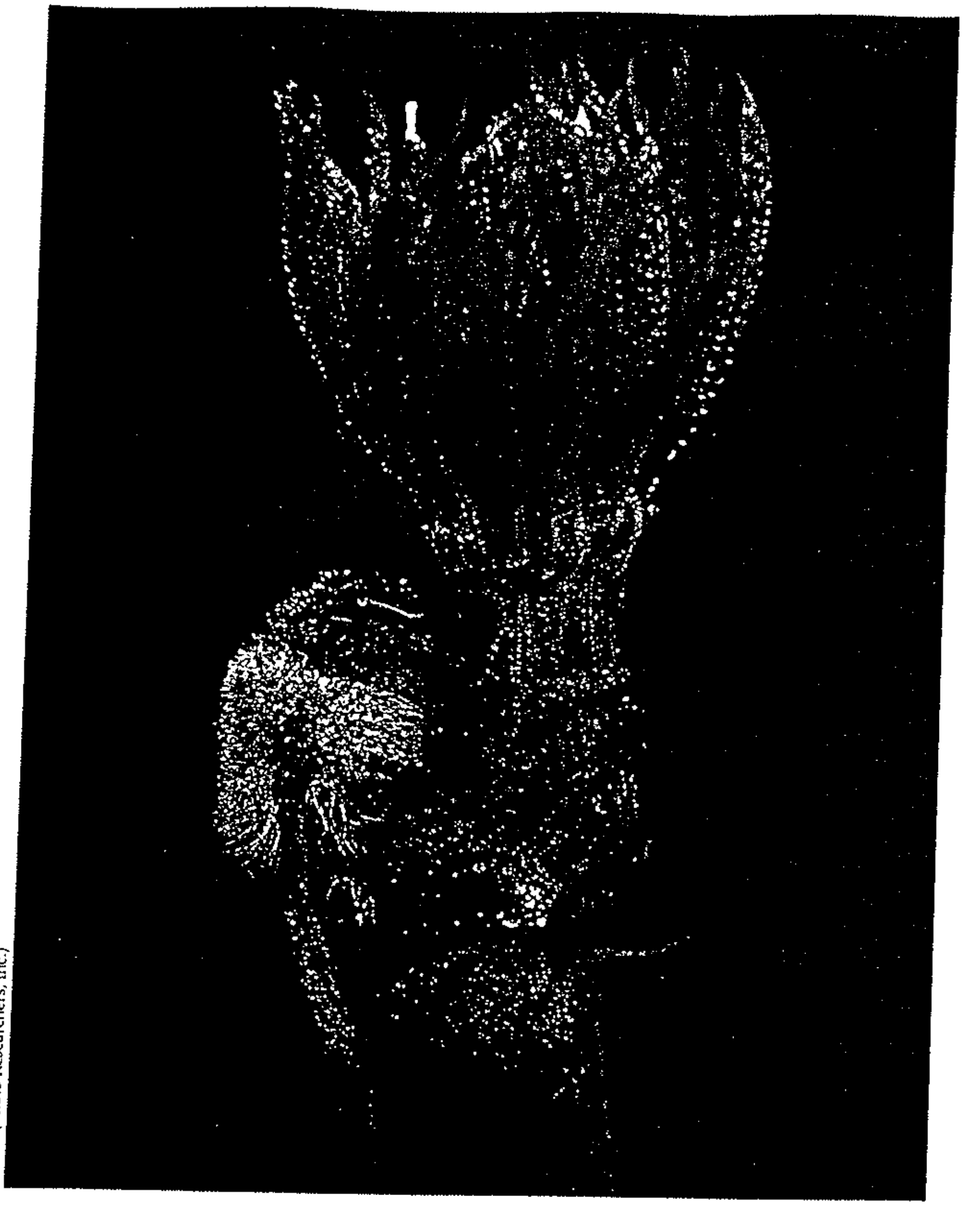
the ambient temperature is five degrees, whereas flying bumblebees have a thoracic temperature of 35 to 40 degrees Celsius and an abdominal temperature of only 15 degrees.

The mechanism behind abdominal and thoracic temperature regulation in bumblebees depends on their circulatory anatomy and physiology. The system involves two structures: the heart and the ventral diaphragm. A bumblebee's heart lies beneath the upper surface of the abdomen. It pumps blood into the thorax through the aorta. The aorta bends down sharply in the abdomen's anterior, forms a ventral loop that passes through the petiole and into the thorax, then curves up between the flight muscles and, finally, into the head. In general, the heart pumps blood anteriorly. The ventral diaphragm, a thin flap of muscle, originates at the petiole and extends over a blood-filled space on the "floor" of the abdomen. The ventral diaphragm undulates toward the rear, pushing blood to the back and sides of the abdomen. It forms a valve at the petiole: When the diaphragm is up, blood passes from the thorax to the abdomen, and when it is down, blood cannot enter the abdomen.

Blood is warmed in the thorax by the flight muscles, and it cools in the abdomen. Near the petiole, the cool blood from the heart enters the thorax and passes near the warm blood entering the abdomen, forming a sort of counter-current heat exchanger, and some of the heat should be returned to the thorax. Relatively little heat reaches the abdomen during preflight warm-up, presumably because of both long periods without a heartbeat and the counter-current heat exchanger. Circulation, however, cannot be cut off indefinitely because the thoracic muscles must be supplied with fuel from the honey-stomach.

A bumblebee, however, can heat up its abdomen. For example, if a bumblebee's thorax is heated to about 42 degrees Celsius, the abdominal temperature may increase sharply. But if the heart is made inoperable, the thoracic temperature soars to lethal levels without causing appreciable heating of the abdomen. In other words, abdominal heating arises from blood circulation.

What circumvents the counter-current system, allowing the abdomen to heat up? Heinrich produced data that support an alternating-current flow that could partially neutralize the counter-current system. According to his model, a bumblebee shuttles blood



L. West (Photo Researchers, Inc.)

Figure 6. Bumblebee has a "fur coat" that helps keep it warm in a cold environment. In fact, the fur cuts heat loss in half. These bees also generate heat through behavioral and physiological mechanisms *(Figures 7 and 8)*.

theless, bumblebees need other mechanisms to keep warm because they live in cold environments.

Bumblebees have a second thermoregulatory task that, at times, necessitates abdominal heating. Like all social bees, bumblebees heat their nest to enhance the growth rate of their young. The congregating of thousands of honeybees in a nest keeps the brood warm. But bumblebee colonies are started anew each spring by a single, overwintered queen, and a lone bumblebee starting a nest on a frosty mountain meadow or on the Arctic tundra cannot heat the entire nest cavity. Instead, she heats her brood through direct body contact, like a brooding bird. An incubating bumblebee elongates her abdomen and wraps it around the brood.

Although previous investigators supposed that the queen was warming herself from the brood, our results confirm that the queen is incubating. When an incubating bee is removed, a brood clump returns quickly to ambient temperature; when a bee returns to incubate the brood, its temperature increases to about 30 degrees Celsius. Experiments in which a dead bumblebee's abdomen or thorax is heated artificially show that only the abdomen effectively heats the brood. Incubating bumblebees (queens, workers and even drones incubate) regulate both their abdominal and thoracic temperatures. In the laboratory, incubating queens of the species *Bombus vosnesenskii* maintain abdominal temperatures around 30 degrees Celsius even when

Figure 7. Incubating queen bumblebee wraps her abdomen around her brood to keep it warm. During incubation, the queen heats her abdomen. In our laboratory, an incubating queen's abdominal temperature was 30 degrees Celsius in ambient temperatures as low as 5 degrees. (Photograph by the authors.)

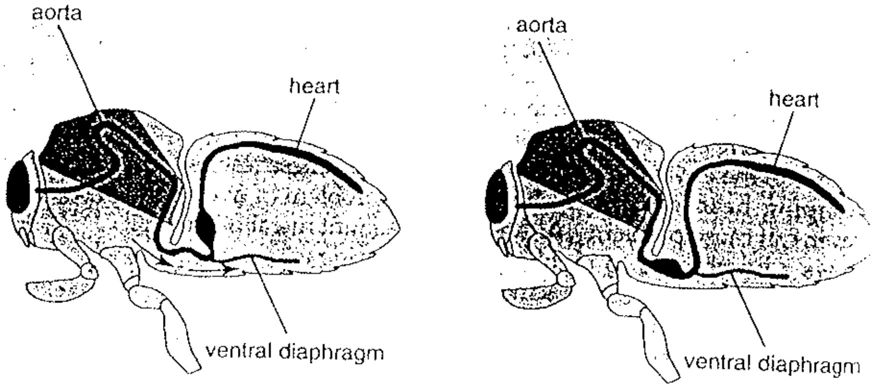
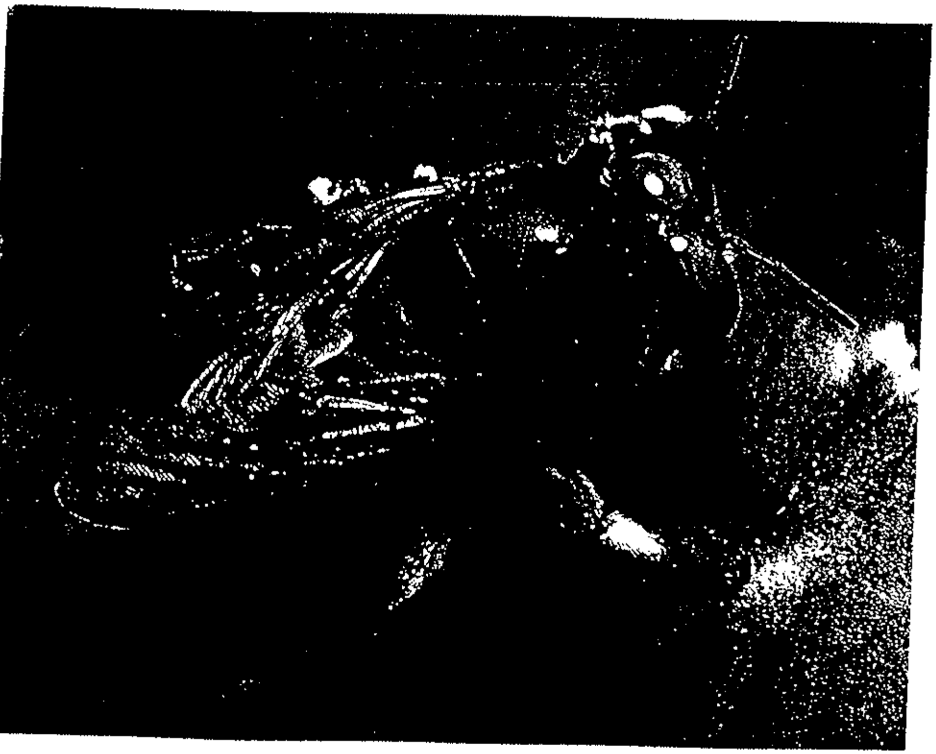


Figure 8. Alternating-current circulatory system allows a bumblebee to regulate the te perature of its abdomen and thorax. The heart pumps blood from the abdomen to the ao in the thorax, and the blood empties into the body cavity in the head. Movements of t ventral diaphragm push the blood in the open body cavity back into the abdomen. At t petiole, cool blood flowing through the heart from the abdomen passes near warm bod cavity blood from the thorax. Little heat is exchanged because pulses of warm blood mo ing from the thorax to the abdomen *(left)* alternate with pulses of cool blood from t abdomen to the thorax *(right)*.

through the petiole, or into and out of the abdomen, in alternating pulses of warm and cool blood. A pulse of warm blood enters the abdomen, then a pulse of cool blood enters the thorax and so on, a sequence of events that eliminates the simultaneous counter currents necessary for heat exchange. Consequently the abdomen heats up.

As this model predicts, an overheated bumblebee shows a series of physiological effects. First, its abdominal temperature increases in tiny, discrete steps that correlate exactly with the mechanical beats of the ventral diaphragm. In other words, each beat of the diaphragm admits a pulse of warm blood into the abdomen. Second, the abdominal heart pumps in discrete pulses (rather than the rapid fibrillations that would produce a continuous flow of blood) at the same frequency as the diaphragm beats. Third, abdominal pumping, or breat ing motions, also assumes the same fr quency as the diaphragm's beats. Th in-out pumping of the abdomen vent lates the muscles and helps pump blo into and out of the abdomen.

A bumblebee's abdomen may b heated during incubation or fligh Some bumblebees generate as much a 33 degrees Celsius of excess heat whe flying at an ambient temperature o



J. H. Robinson (Photo Researchers, Inc.)

Figure 9. Carpenter bee uses its head to fly on the hottest desert days. The large head holds the bee's massive mandibles, which it needs to chew through wood. In addition, the head's large surface provides convective cooling.

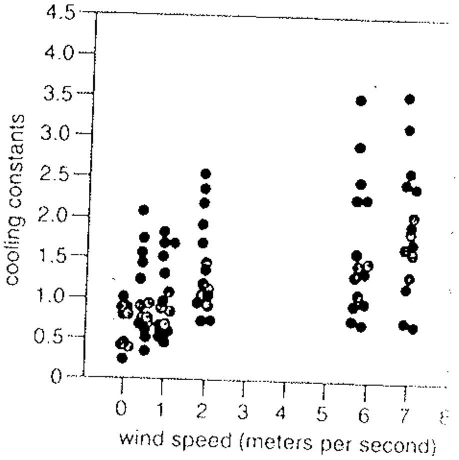


Figure 10. Convective cooling in carpente bees increases at higher wind speeds. As wind speed increases from 0 to more than 6 meters per second, the cooling constants (degrees Celsius of convective heat loss per minute for each degree of temperature difference between the head and the environment) for the bee's thorax *(red)* and abdomen *(yellow)* roughly double. Over the same increase in wind speed, the head's cooling constant *(blue)* increases by about six times. Therefore a carpenter bee loses more heat through convection when it flies faster.

only two degrees. At higher ambient temperatures, some of this flight-produced heat must be released. Perhaps a major portion of the heat loss is accomplished by dumping the excess into the abdomen, where convection dissipates the heat into the environment.

Dumping heat into the abdomen, however, can cause problems. Although it allows a bumblebee to incubate its brood and to fly at higher air temperatures, heat loss through the abdomen could be a problem at lower air temperatures. The "imperfect" counter-current heat exchanger, which is designed to leak in some cases, can never retain all the thoracic heat. Indeed, bumblebees foraging at low air temperatures do have a considerable amount of heat leaking into their abdomen. The "fur coat" comes into play here as an insulator. The overall design generates a thermal strategy that incorporates social and individual needs.

Free Cooling

Carpenter bees—the ones that bore tunnels in solid wood—must cope with high temperatures in their hot desert environment. They might be expected to have trouble preventing overheating for three additional reasons. First, they are among the largest bees known, some weighing two grams. Second, they fly in the sunshine at noon on nearly the hottest desert days, when ambient temperatures approach 40 degrees Celsius. Third, carpenter bees have a high wing loading (small wings and a heavy body), so they cannot greatly reduce their power output during flight. How do these bulky, fast fliers avoid overheating?

It appears that a carpenter bee uses convective cooling, largely from its head. A carpenter bee has a large head, carrying a set of massive mandibles and the associated muscles required to chew into wood. The head is flattened and fits, like a cap, on the front of the thorax. During forward flight, the head faces the wind, and convective heat loss is inevitable, providing the head heats up above the air temperature. The smooth contact between the thorax and the head should allow heat to flow freely from the working flight motor into the head. Additionally, fluid flow to the head transports even more heat, like a car's radiator. The head is an effective radiator for the thorax, but how is the heat loss regulated?

Heinrich and Buchmann examined this problem in the desert carpenter bee, *Xylocopa varipuncta*. Surprisingly, the bees flew faster in higher air temperatures. Mark Chappel of the University of California at Riverside also reported that carpenter bees' flight speed increases noticeably as the air temperature increases. These results seem surprising, if the problem of overheating arises from the flight metabolism.

Trying to isolate the possible sources of convective heat loss, we severed the head and abdomen from the thorax and remounted them in their former positions, but without contact. When we measured their convective heat loss, we found that the head is from two to three times more sensitive to variations in wind speed than are the thorax and abdomen. The cooling constant of the head increased from 0.5 to 3.0 degrees Celsius per minute for each degree of temperature difference between the head and the ambient temperature as the wind speed increased from 0 to 6 meters per second. That is, the head's convective heat loss increased by six times. Such heat loss is likely in carpenter bees, because they fly regularly at as much as 12 meters per second.

We speculated from these results that a carpenter bee could cool off by flying faster. There was one problem: The increased convective cooling that comes with faster flight might be offset by an increase in metabolic heat, if flying faster requires a bee to expend more energy.

Until recently, no one had measured the metabolic cost of insect flight as a function of flight speed during free flight. In a technical tour de force, however, Charles P. Ellington of Cambridge University and Timothy M. Casey of Rutgers University created a flight apparatus in which bees fly freely against an air stream, and the oxygen that the bees extract from the air is measured. The device allows Ellington and Casey to measure the metabolic rate (or heat production) of freely flying bees as a function of flight speed. (Although the bumblebees flew in place, their flight speed was controlled by varying the speed of the air stream.) The results reveal that the metabolic cost of flight in bumblebees is independent of flight speed. Unless a carpenter bee's aerodynamics and flight mechanics are vastly different from a bumblebee's (which they resemble closely in morphology), there is no added heat production with increasing flight speed. In other words, carpenter bees probably get "free" cooling simply by flying faster.

In the past, many investigators believed that only the "higher" vertebrates had achieved the evolutionary pinnacle of a regulated, high body temperature. Through sophisticated experimental techniques, however, the world of insect thermoregulatory capabilities has been opened, and bees are particularly noteworthy. We propose that the thermoregulatory virtuosity of bees rivals that of human beings.

Bibliography

Esch, H., and F. Goller. 1991. Neuronal control of honeybee fibrillar muscle during shivering and flight. *Journal of Experimental Biology* 159:419–431.

Esch, H., F. Goller and B. Heinrich. 1991. How do bees shiver? *Naturwissenschaften* 78:325–328.

Goller, F., and H. Esch. 1990. Oxygen consumption and flight muscle activity during warm-up and free flight. *Journal of Comparative Physiology* 96:155–166.

Heinrich, B. 1979. *Bumblebee Economics*. Cambridge, MA: Harvard University Press.

Heinrich, B. 1979. Keeping a cool head: honeybee thermoregulation. *Science* 205:1269–1271.

Heinrich, B., ed. 1981. *Insect Thermoregulation*. New York: Wiley.

Heinrich, B. 1993. *The Hot-Blooded Insects*. Cambridge, MA: Harvard University Press.