Part **XII**

Animal Diversity

Honeybees are endotherms. By adjusting metabolic rates in their flight muscles, honeybees are able to maintain their body temperature within a narrow range.

Real People Doing Real Science

How Honeybees Keep Their Cool

One of the biggest problems terrestrial animals face is that the temperature of their environment keeps changing. Why does changing temperature present a problem? The structures of many of the body's enzymes and regulatory proteins rely on weak chemical bonds, and a change in temperature easily disrupts them, changing their shape and perturbing their function. A decrease or increase of only a few degrees can have a significant impact on metabolism, and great changes in temperature can be fatal.

Terrestrial organisms have taken two very different approaches to confronting the problem posed by changing temperatures. On the one hand, many species have evolved the ability to maintain their body temperature within a narrow range, regardless of the temperature of their surroundings. We call such organisms endotherms. Birds and mammals are the primary examples of this strategy, but certain invertebrates are also endotherms. Because the costs of maintaining a stable body temperature are considerable (90% of your food intake must be expended just to produce heat), the majority of organisms elect instead to allow their body temperature to conform closely to their surrounds. These organisms are called ectotherms.

Imagine you were standing in a high mountain meadow on a cool sunny morning, with butterflies and bees flying about among the flowers. A cloud obscures the sun, blocking its warming rays. The butterflies immediately settle to the ground and wait for the sunlight they need to keep warm enough to fly. Not the bees. They keep zipping around from flower to flower, heedless of the loss of the sun's warmth. How does the bee manage this? Bees are one of the few invertebrates that are endotherms. Aloft, they keep their body temperature relatively constant, whatever the temperature of the air through which they are flying.

How does the bee—or any endothermic animal—generate the heat needed to warm itself? About 75% of the energy content of the chemical bonds in an animal's foodstuffs is dissipated as heat during metabolism. Thus no new type of metabolic scheme is required to be an endotherm. Instead, an endotherm revs up the metabolic reactions it already has, finding ways to increase the flux through its preexisting food-burning pathways.

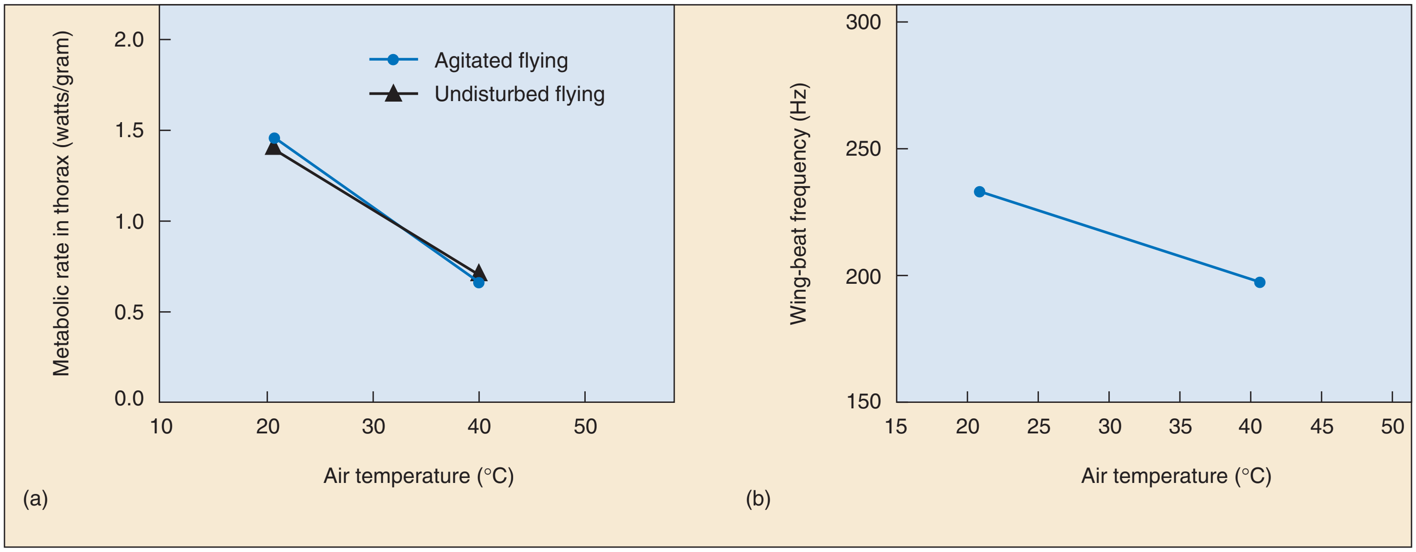
When a bee wants to fly, it first shivers violently, often for several minutes. This burning of glucose generates the heat needed to become airborne. Once aloft, the flight muscles generate enough heat to maintain the bee's body temperature within the range required for flight.

So what happens if the sun *stays* out, warming everything hotter and hotter? Eventually the butterflies settle back to the ground in cooler shady spots, avoiding sunlight and waiting for cooler moments. Not so the bees. They keep right on flying, again oblivious to the sun.

How do these bees avoid overheating? Researchers studying bumble bees thought they had the answer. Bumble bees have large abdomens, devoid of insulation, which radiate heat very effectively. When the bumble bee is not flying (and little heat is being produced), there is little flow of heat from the thorax. When the bumble bee starts to fly, heat is carried from the flight muscles of the thorax to the abdomen by blood (called hemolymph), which circulates in response to the body's movements. In effect, the bumble bee has an endothermic thorax and an ectothermic abdomen which acts as a heat dissipater.

However, when researchers looked at honeybees (the kind of bees flying in our mountain meadow), this explanation doesn't work. It turns out that transfer of heat between thorax and abdomen is not an important mechanism for regulating body temperature in flying honeybees. So how do honeybees keep cool while flying?

In stationary animals including birds, variation in metabolic heat production is an important mechanism of thermoregulation (witness shivering in response to cold). This mechanism, however, was thought to be unavailable to flying animals. Flight requires a huge expenditure of energy to keep the animal airborne, and the metabolic costs of flight are commonly thought to be determined by factors such as the animal's weight, wing area, flight speed, etc. How could a flying animal vary metabolism for thermoregulation and at the same time accomplish flight?



Effects of air temperature on metabolic rate and wing-beat frequency. (*a*) While the air temperature was increased from 20° to 40°C, metabolic rates of honeybees were determined by measuring carbon dioxide emissions in bees that were agitated to keep them flying (dots) and in bees that were allowed to fly undisturbed (triangles). In both cases, the metabolic rate dropped with increasing temperatures. (*b*) The wing-beat frequency was determined by measurements made with digitized tape recordings. The wing-beat frequency decreased with increasing temperatures.

The Observation

In an experiment designed to compare the flight metabolic rates of African and European honeybees, Jon Harrison (Arizona State University) and H. Glenn Hall (University of Florida) discovered that relatively small increases in air temperature were correlated with substantial decreases in flight metabolic rate and wingbeat frequency. This result suggests the hypothesis that honeybees may be able to vary their metabolic rate by changing flight muscle performance, and in this way achieve thermoregulation. However, the observed correlation might have other explanations. The air temperature variation in this study occurred as temperatures varied within and across days. Perhaps bees that fly in the afternoon, when it is warm, are simply a different age or genetic makeup than bees that fly in cooler weather. A manipulative experiment is required to rigorously test the hypothesis.

The Experiment

To test this hypothesis, Dr. Harrison and a team of researchers randomly exposed honeybees to various air temperatures between 20° to 40°C, and measured thorax and abdominal temperature, metabolic rate, and wingbeat frequency. Body temperatures were taken with a tiny, fast-responding microprobe. Metabolic rates were measured by flowing air through the bee flight chamber at a known rate, and measuring the release of carbon dioxide by the bee. Wingbeat frequency was measured using a microphone, tape recorder, and sound-editing software.

The Results

Can flying honeybees vary heat transfer between thorax and abdomen like bumblebees? If honeybees thermoregulate the thorax by varying heat transfer between thorax and abdomen, then lots of heat should be transferred from the thorax to the abdomen when the bee flies in warm air, but little heat should be transferred when the air is cold. In this experiment, thorax temperatures varied much less than air temperature. Clearly, theses honeybees did not thermoregulate like bumblebees.

Can flying honeybees vary metabolic heat production with air temperature? Flight metabolic rates decreased 40 to 50% in bees flying in 40°C air compared to 20°C air (graph *a* above). This indicates that honeybees maintain warm, relatively constant thorax temperatures by producing lots of metabolic heat at cool air temperatures, and much less metabolic heat when flying in warm air.

How can honeybees vary metabolic heat production and still hover? Harrison and his colleagues found that the wingbeat frequency of the hovering honeybees fell by 16% as air temperature increased (graph *b* above). These results suggest that honeybees may vary heat production by varying flight muscle power in a manner somewhat comparable to heat production by shivering muscles in mammals. According to this hypothesis, bees in colder air are able to utilize more metabolic fuels and produce more heat because the flight muscles work harder and use more ATP. Experiments to rigorously test this remarkable mechanism remain to be done.