nisms of disease.

I hope that a wise spirit prevails at Yale and at other universities who will counsel undergraduate majors in any area of biology to take the classes they need to understand the full sweep of life, regardless of current or future departmental boundaries.

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Honeybee Thermoregulation

In the report "Achievement of thermal stability by variation of heat production in flying honeybees" (4 Oct., p. 88), Jon F. Harrison *et al.* conclude that "variation in heat production may be the primary mechanism for achieving thermal stability in flying honeybees, and this mechanism may occur commonly in endothermic insects." Their conclusions are based on results derived from bees said to be in "high-intensity, agitated flight." It is difficult to achieve uninterrupted flight in a confined space (*1*). We and others (*2*), have long wrestled with this problem. Harrison refers to "agitated flight" (presumably by shaking the vessel so bees would remain airborne) or "undisturbed hovering." We doubt that "agitated flight" represents "high-intensity flight." Given the experimental conditions, it is likely that bees interrupted their flights frequently for several hundred milliseconds at a time. At low ambient temperatures, they would have shivered during interruptions, elevating apparent metabolism during flight.

We observed bees flying without interruption in a wind tunnel (*3*), with realistic lifts and thrusts only at wind speeds of several meters per second and with optical patterns simulating appropriate ground speeds. We observed only short bursts of flight when the bees' thorax temperatures were between 36° and 40°C. Bees shivered between flights at ambient temperatures below 35°C. Above 35°C, their muscle potentials (and active energy expenditure) stopped completely during flight interruptions.

Hovering flights could only have lasted for a few seconds in the small vessels used by Harrison *et al.* Muscle activity before and after the short hovering bouts must have affected the measurements, even when the flow rates of air through the respiratory vessels were fast.

Variation of heat loss and heat production are, of course, not mutually exclusive. However, the data presented by Harrison *et al.* do not show regulation of heat production for thermoregulation during flight.

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Harrison *et al.* find an inverse relation between metabolic rate and ambient temperature for both agitated and undisturbed honeybees in flight. They conclude that honeybees may accomplish thermoregulation primarily by varying heat production. These findings are not consistent with those of several other laboratories. Also, there appears to be internal inconsistency in the reported data.

Previous measurements of honeybee metabolic rate during flight have ranged from 40 to 60 milliwatts, with no apparent temperature effect found between 20° and 40°C (*1*–*3*). One study sought and did not find an effect of ambient temperature on flight metabolic rate in honeybees (*1*). Yet Harrison *et al.* find lower metabolic rates during flight at higher temperatures, especially at 38°C (their table 1 and figure 3A), where values are about half of those previously observed. They suggest that their use of open-flow respirometry might have yielded more accurate measurements than previous closed-chamber, and therefore integrative, measurements (*1*). The superior temporal resolution of open-flow respirometry would afford better isolation of flight from brief periods of rest, possibly yielding higher, but certainly not lower, values for metabolism during flight. Respirometry methods alone do not account for this difference.

Possible alternative explanations include the small chamber size (300 milliliters) and brief (1 minute) equilibration and measurement periods (*4*, *5*), which contrast with those found in previous studies (*1*–*3*). Harrison and Hall have noted (*4*) that metabolic rates of agitated, flying honeybees in 300-milliliter chambers declined if the measurement period was prolonged beyond 1 minute (*4*), leading us to question whether the data obtained are as representative of natural flight or hovering as those made in far larger chambers (*1*, *3*) or in wind tunnels (*2*). In addition, the values in figure 1A of Harrison *et al.*'s report—in which data for agitated European, African, and hybrid honeybees are pooled—are consistently about 25% higher than values observed for agitated European bees in their figure 3A. This suggests that there may be inconsistency between methods used in the two data sets.

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Response: With regard to the comment by Stevenson and Woods, the respirometric methods (including chamber size and flight times) were the same throughout our study, so methodology is unlikely to account for the differences in metabolic rate seen in figures 1A and 3A of our report. The most likely explanation for these results is genetically based differences in metabolic rates among the honeybee stocks used. Figure 1A of our report included data for African honeybees, which have metabolic rates during flight that are about 10% higher than those of European honeybees (*1*). Cytoplasmic malate dehydrogenase, a glycolytic enzyme, exhibits a cline in honeybees on three continents; honeybees found at low latitudes possess a higher concentration of the electrophoretically fast allozyme, while honeybees sampled at high latitudes have higher concentrations of the electrophoretically moderate allozyme (*2*). Two studies have shown that the electrophoretically fast allozyme is associated with higher metabolic rates within European worker honeybees, with rate differences between the stocks ranging from 2 to 25% (*3*, *4*). Also, in a study of intercolonial variation in metabolic rates during flight, we found that worker bees from two adjacent, similarly sized colonies had rates that differed by up to 18% (*4*). Because of the large variation in such rates that can occur among colonies as a result of genetic and environmental effects, the differences in rates, as seen in figures 1A and 3A of our report, are not unexpected.

Similarly, the large genetic and environmental effects on honeybee metabolic rates during flight may explain why there is no obvious effect of air temperature in the studies of honeybee flight metabolism cited by Stevenson and Woods (*4*, *5*). These studies used different air temperatures (which ranged from only 21° to 32°C).

Both comments state that the metabolic rates we reported may not accurately reflect those achieved during flights of long duration, especially with the small (0.3 liter) chamber we used in the "agitated flight" assays. We conducted a study of "hovering flight" (our report, figure 3A) to address this concern. For these experiments, the chamber volume was 2 liters, and mean flight time was 3.5 minutes. Only data from bees that hovered continuously without provocation were used. For the studies cited by Stevenson and Woods (*3*, *5*, *6*), chamber volumes (mean = 2.0 liters, range = 0.8 to 4 liters) and flight times (mean = 5.3 minutes, range = 3 to 8.7 minutes) were similar to those we used. We found that air temperature had the same effect on metabolic rate during flight in assays of "hovering flight" of long duration in a large chamber as in the assays of "agitated flight" of short duration in a small chamber (our figure 3A).

We have since used closed-system respirometry with 0.551-liter chambers and flight times of 6 minutes to measure flight metabolic rates. At 45°C, these rates were approximately 48% lower than those measured at 21°C (7). Thus, neither chamber size nor flight duration appears to affect our conclusion that metabolic rate during flight decreases strongly at higher air temperatures in honeybees.

Stevenson and Woods also state that the metabolic rates we reported at 38°C were "unusually low." Only Heinrich's study (6) has reported metabolic rates during honeybee flight at high (38° to 40°C) air temperatures. The values we observed at 38° to 40°C were 13% below those reported by Heinrich. However, at 20° to 21°C, the values we observed exceeded those reported by Heinrich by 48%. Thus, the major difference between Heinrich's results and ours occurred at low air temperatures and were associated with higher metabolic rates during flight in our study. In Heinrich's study, metabolic rates during flight were measured after carbon dioxide narcosis and tarsectomy. If flight or thermoregulatory behavior degrades with the stress of anesthesia or surgery, this may account for the lower metabolic rates he observed at 20° to 21°C.

In the three independent experiments described in our report and in a subsequent closed-system respirometry experiment (7), we used three different respirometric methods, four different genetic stocks of honeybees, and more than 700 bees. The metabolic rates during flight that we measured at 38° to 45°C were 40 to 50% lower than those we measured at 20° to 21°C. The fact that wingbeat frequency also decreases over this temperature range [our report and (8)] provides strong, support for a thermal effect on flight behavior and metabolic heat production in honeybees. Similar effects of air temperature on metabolic rate during flight and wing beat frequency during hovering have been found for the solitary bee *Centris pallida* (9). These findings necessitate a reevaluation of the conclusion made in reviews (10) that flying endothermic insects thermoregulate primarily by varying heat loss.

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Letters to the Editor

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