THERMOREGULATION AND ENERGETIC DECISION-MAKING BY THE HONEYBEES *APIS CERANA, APIS DORSATA* AND *APIS LABORIOSA*

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Summary

Thoracic flight temperatures (T_{th}) of workers of three species of honeybees (genus *Apis*) in Nepal were measured at relatively low ambient temperatures (T_a). At $T_a=18$–24°C, *A. dorsata* workers arriving at feeders to collect concentrated ($\geqslant 40$%) sugar syrup maintained higher temperature gradients $(T_{th}-T_a)$ than workers arriving at feeders with dilute (6–17%) syrup. Temperature gradients were inversely related to T_a, indicating thermoregulation at low T_a. Similarly, temperature gradients varied inversely with T_a in *A. cerana* and *A. laboriosa* workers arriving at feeders at $T_a=12$–20°C. Temperature data suggest that honeybees have the ability to regulate heat production in flight and that they may vary their flight efforts according to expected gains and associated costs. Temperature gradients of *A. laboriosa* workers in flight are apparently about the same as those of *A. mellifera* workers, whose body mass is only half that of *A. laboriosa*. The circulatory systems of *A. laboriosa* workers show no striking differences from those of other species of *Apis* and are therefore probably equally effective at retaining heat in the thorax. This suggests that the relatively low (in relation to the body size) $T_{th}-T_a$ maintained by *A. laboriosa* may be an indication of a relatively low metabolic rate and consequent low heat production. This is supported by an analysis of mass$^{1/3}$-specific wing-loading and, in turn, suggests that *A. laboriosa* may be grouped with *A. dorsata* and *A. florea* as a relatively low-powered, open-nesting honeybee, in contrast to the more high-powered cavity-nesters, *A. cerana* and *A. mellifera*.

Introduction

In general, the ability of endothermic insects to maintain an elevated thoracic temperature in flight is strongly size-dependent (reviewed by Bartholomew, 1981). The gradient in flight between thoracic (flight muscle) temperature (T_{th}) and ambient temperature (T_a) is usually greater for large insects than for small insects. The phylogeny of a species and adaptations by that species to a particular thermal environment may have important influences on body temperature, however (Stone and Willmer, 1989*b*). In addition, individuals of eusocial species may be

affected by selective pressures operating at the colonial as well as the individual level (Dyer and Seeley, 1990).

In a study of endothermy and body size in honeybees (genus *Apis*), Dyer and Seeley (1987) found that four species (*A. cerana*, *A. dorsata*, *A. florea* and *A. mellifera*) deviated from predicted size-dependent energetic patterns. Their analysis revealed a parallel dichotomy in worker physiology and colony nesting behavior. The open-nesting *A. florea* and *A. dorsata*, the smallest and largest species studied, were similar to each other in having relatively low metabolic rates and being relatively low-powered in comparison with the cavity-nesting *A. cerana* and *A. mellifera*. Dyer and Seeley (1990) suggest that the cavity-nesting species have been selected to have faster-paced, higher-powered workers in order to take advantage of a greater rate of output made possible by the cavity-nesting lifestyle.

The Himalayan honeybee *Apis laboriosa* builds its nests in the open on sheer cliffs in mountainous regions of Bhutan, China, India and Nepal (Sakagami *et al.* 1980). Depending upon the season of the year, *A. laboriosa* colonies nest at altitudes of 1200–3500 m (Underwood, 1990), a range that includes the warm temperate to subalpine climatic zones (Kawakita, 1956).

What follows here is an investigation of worker energetics designed to explore whether *A. laboriosa* conforms to the pattern discovered by Dyer and Seeley (1987) for other open-nesting honeybees or whether it departs from that pattern, perhaps as a result of adaptations to the relatively harsh environment in which colonies live. Data gathered for *A. laboriosa* suggested that worker honeybees have more control over their energetic expenditure than previously thought. This necessitated the collection of additional data for *A. cerana* and *A. dorsata* so that the several species of honeybees in Nepal could be compared more directly with those elsewhere.

Materials and methods

Time frame and study site

Data presented here were collected between December 1987 and February 1989. Most of the study was conducted in Kaski District, west-central Nepal, and was centered around the village of Chhomrong (altitude 1980 m) and a higher-altitude (2530 m) site known as 'Dovan'. In December 1988, 2 weeks were spent at the Institute of Agriculture and Animal Science (IAAS) in Rampur, Chitwan District in south-central Nepal. The campus of the IAAS is about 120 km southeast of Chhomrong and is at an altutide of about 240 m.

Body mass

Samples of freshly killed bees were weighed to the nearest 0.01 g on a small, portable balance (Ohaus). Unless otherwise noted, reported masses are averages of 50-bee samples of unengorged workers either captured arriving at feeders (for *A. cerana*, *A. dorsata* and *A. laboriosa*) or (for *A. laboriosa* only) taken from the surfaces of winter clusters (see Underwood, 1990).

Thoracic mass is used for some comparisons; thoraces (pooled samples of 50–71) were weighed after detachment of the wings and legs.

Training bees to feeders

Bees were trained to feeders consisting of a glass jar inverted over a grooved Plexiglas base (see von Frisch, 1967) and offering scented sugar solution (6–50 % sugar by weight). All the temperature data for *A. laboriosa* arriving at a feeder were collected at Dovan during the month of July. The weather at that time was nearly always overcast and bees frequently arrived at the feeder in a light rain. To ensure that bees continued to visit the feeder in sufficient numbers, the syrup was kept relatively concentrated (25–50 % sugar) and the feeder was often crowded.

At Dovan the feeder was located about 500 m from a cliff on which several colonies of *A. laboriosa* nested. *Apis cerana* workers trained to the same feeder came from a feral colony in the forest also about 500 m away. Feeders to which *A. cerana* workers were trained in the village of Chhomrong were located 200–300 m from the colonies. Data on the flight temperature of *A. dorsata* workers were gathered in Rampur, Chitwan District, at a feeder about 150 m from a water tower on which numerous colonies nested.

Temperature measurements

Temperature measurements (to the nearest 0.1°C) were made using a digital thermometer (Sensortek Bat-12) with type K (copper–constantan) thermocouple needle probes (no. 29/1b, 0.3 mm diameter). Thoracic temperatures (T_{th}) of individual bees were taken by grasping the bee by hand and stabbing it immediately (within 3 s) in the center of the thorax with the thermoprobe. Because bees begin to cool immediately after landing, thoracic temperatures obtained by this 'grab and stab' method are slight ($\leqslant 0.5$°C; Stone and Willmer, 1989*a*) underestimates of the actual flight temperatures. Measurement errors would have been similar for the several species or for workers of a single species under varying conditions. Ambient temperatures (T_a) were measured with the same thermo-probe and were taken in the shade after recording T_{th}.

Experiments investigating the effects of differing sugar concentration and of crowding on T_{th} were performed over a 12-day period with *A. dorsata* workers in Rampur. Bees were trained to a feeder station offering either concentrated or dilute syrup. After an acclimation period of at least 20 min, temperatures of arriving bees were recorded. Following a variable period of data collection, the old syrup was exchanged for one differing in concentration and no new data were collected within the 20 min period after such a switch.

All bees for which T_{th} was recorded were dissected to ascertain the amount of liquid in their honey stomachs. If a bee captured arriving at a feeder carried more than about 2–5 μl, it was assumed that she had not come directly from the nest. In such a case, T_a was not taken and the data for that bee were discarded.

Value of thoracic hair to bees in flight

Bees arriving at a feeder were captured and held between the thumb and forefinger of one hand. A pair of watchmaker's forceps was used to rub and pluck the thoracic hairs from the bee. After most (an estimated 90 %, excluding that on the legs) of the thoracic hair had been removed, the bee was given a color-coded mark on the abdomen with a dot of Liquid Paper® and released. Some of the depilated bees (42 of 70 *A. laboriosa* workers thus treated were recovered) later returned to the feeder and their thoracic temperatures were measured.

To determine if depilated bees could produce heat normally, the thoracic temperatures of *A. laboriosa* workers preparing to leave the feeder were measured. After a bee has finished taking syrup from a feeder, she usually backs away a few steps and stands in one place while rhythmically pumping her abdomen. She then grooms her eyes and antennae before taking off. Take-off temperatures are T_{th} measurements of bees grasped as they groomed their antennae.

Whether from arriving bees or from those about to depart, data from depilated bees were paired with those from intact bees in a similar state captured within seconds or minutes of each other. Ambient temperature never differed by more than 0.4°C for the bees within any one pair.

Passive cooling rates

The cooling rates of freshly killed *A. laboriosa* workers were measured (in a draught-free room) with a thermoprobe inserted into the thorax so that the probe's tip was near the center. The probe lead was affixed to a wooden stand, holding the impaled bee about 10 cm above a table top. The bee was then heated with the beam of a microscope lamp focused on its thorax. As T_{th} reached about T_a+23°C, the heat source was removed quickly and the bee began to cool. For a period of 180 s after it reached exactly T_a+22°C, T_{th} was recorded at 4-s intervals. The insulating qualities of the thoracic hair were investigated by shaving the thoraces of some bees before measuring their cooling rates. In all cases, T_a was measured both before impaling a bee and after removing her from the probe; in no instance did T_a vary by more than 0.3°C during the measuring period.

Because of the need for a reliable source of electricity, measurements of the cooling rates were made in Kathmandu (altitude about 1250 m). This required the transport of live specimens from the main study area, a 3- to 5-day journey.

Wing-loading

Wings from nine *A. laboriosa* workers were severed from the bodies and mounted on glass slides under coverslips. A Calcomp digitizer (high-accuracy model) was used to measure the wing areas (measurements performed by Acrotek, Ithaca, New York). Wing-loading (in $N\,m^{-2}$) was calculated according to the formula $M_b g/A$, where M_b is body mass in kg, g is the acceleration due to gravity (9.8 m s^{-2}) and A is the area of the wings in m^2.

Dissections of circulatory systems

In honeybees, the aorta makes a series of about 8–10 loops as it passes through the petiole (Snodgrass, 1956; Dyer and Seeley, 1987). This morphological feature is thought to restrict the loss of heat from the thorax as hemolymph warmed by the flight muscles passes into the abdomen (Heinrich, 1980b). To determine if *A. laboriosa* workers possess this feature, live individuals were dropped into a picrol–formal solution and specimens thus preserved were later dissected.

Results

Body mass

Table 1 lists some traits of three species of honeybees in Nepal and compares these with values obtained by Dyer and Seeley (1990) for two of the species in Thailand. *Apis laboriosa* is the largest of the world's honeybees, its workers weighing on average about 40 % more than *A. dorsata* workers. The known variation in body size among *Apis* spp. thus includes an approximately sevenfold range from *A. florea* (22.6 mg; Dyer and Seeley, 1987) to *A. laboriosa* (165.4 mg). Workers of *A. dorsata* in Nepal were slightly (about 5 %) smaller than those in Thailand, but *A. cerana* workers in Nepal were about 26 % larger than their Thai counterparts.

Thoracic masses of workers of both *A. laboriosa* and *A. dorsata* in Nepal were nearly exactly (within 1 %) as would be predicted from their body sizes by the regression ($y=0.254x^{1.09}$) calculated by Dyer and Seeley (1990). For *A. cerana*, however, the thoracic mass of the Nepalese bees exceeded the predicted value by more than 20 % (24.4 *vs* 20.0 mg).

Thoracic temperature

Temperature data for *Apis laboriosa* workers arriving at the Dovan feeder (overcast conditions) and at a winter cluster near Chhomrong (sunny weather) are

Table 1. *Some energetic and physical traits of workers of* Apis cerana, A. dorsata *and* A. laboriosa

Trait	A. cerana Thailand*	A. cerana Nepal	A. dorsata Thailand*	A. dorsata Nepal	A. laboriosa Nepal
Mean body mass (mg)	43.8	55.0	118.0	112.6	165.4
Mean thorax mass (mg)	15.3	24.4	45.5	43.8	66.1
Mean $T_{th}-T_a$ (°C)	11–16	17–21	9–12	9–16	15–21
Maximum crop volume (μl)	34.3	ND	108.4	ND	164.0
Wing loading ($N\,m^{-2}$)	13.02	ND	12.61	ND	14.51
Wing loading$\times M_b^{-1/3}$ ($N\,m^{-2}\,kg^{-\frac{1}{3}}$)	369.4	ND	257.1	ND	264.3

*Data for Thai bees from Dyer and Seeley (1990).

M_b, whole body mass; T_a, ambient temperature; T_{th}, thoracic temperature in flight; ND, not determined.
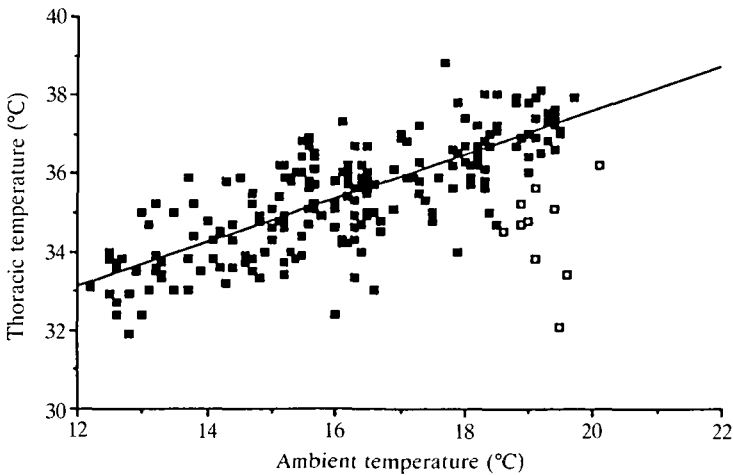
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Fig. 1. Thoracic temperatures of *Apis laboriosa* workers arriving at the Dovan feeder (■; overcast skies, rich syrup) and at a winter cluster near Chhomrong (□; sunny weather). Regression line (calculated from the Dovan data only): $y=26.47+0.553x$, $r^2=0.58$, $P<0.001$, $N=204$.

presented in Fig. 1. The regression calculated from the Dovan data is highly significant ($P<0.001$) and the regression coefficient differs significantly from both 0 and 1 ($P<0.001$ in each case, test for significance of regression coefficients; Sokal and Rohlf, 1987). Thus, the bees were maintaining neither a constant T_{th} nor a constant $T_{th}-T_a$ over the range of $T_a=12.2–19.7°C$. Temperature gradients of bees returning to the winter cluster ($N=10$) were lower (15.3 ± 1.25 *vs* $18.1\pm0.72°C$, mean$\pm$s.D. $P<0.001$, *t*-test) than those of Dovan bees ($N=49$) arriving at the feeder at comparable ambient temperatures, despite the more favorable weather conditions near Chhomrong.

Fig. 2 compares the T_{th} of *A. cerana* workers arriving at feeders at Dovan and in Chhomrong. In each case, the calculated regression coefficient differs significantly from both 0 and 1 ($P<0.001$, each of four cases). Over a range of $T_a=12.3–19.6°C$, *A. cerana* workers arriving under overcast skies had significantly lower (mean difference approx. $1.9°C$) T_{th} than those arriving in sunny weather [$P<0.001$, analysis of covariance (ANCOVA); Sokal and Rohlf, 1987]. Thoracic temperatures of *A. cerana* workers at Dovan were also significantly lower (approx. $1.5°C$) than those of *A. laboriosa* workers a Dovan ($P<0.001$, ANCOVA).

Flight temperature data from *A. dorsata* workers arriving at feeders in Rampur, Chitwan District (altitude about 240 m), are presented in Figs 3 and 4 and in Tables 2 and 3. Foragers arriving at feeders offering concentrated syrup had significantly higher T_{th} ($P<0.001$, ANCOVA) than those coming to collect dilute syrup (mean difference approx. $2.5°C$, Fig. 3). The regression lines are highly significant ($P<0.001$), with coefficients differing from both 0 (concentrated $P<0.001$; dilute $P<0.02$) and 1 ($P<0.001$ in each case). The temperature gradient maintained varied inversely with T_a (Fig. 4), but the bees did not maintain a constant T_{th}. The

pattern of higher T_{th} (at a given T_a) of bees arriving to gather more concentrated syrup was apparently an effect of the richness of the syrup rather than the degree of crowding at the feeders (Table 2).

Data presented in Figs 3 and 4 and in Table 2 were all collected during fair weather. Under overcast conditions, *A. dorsata* workers arriving at a feeder offering concentrated syrup had about 1.0–1.5°C lower $T_{th} - T_a$ than workers
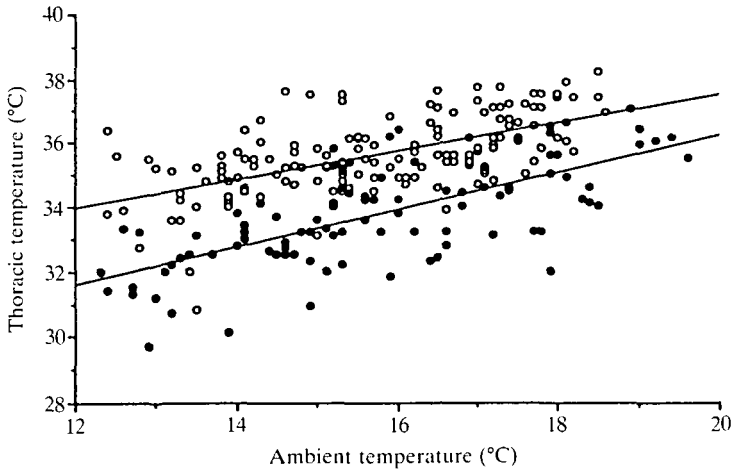

Fig. 2. Thoracic temperatures of *Apis cerana* workers arriving at feeders offering rich syrup at Chhomrong under sunny skies (○) and at Dovan under overcast skies (●). Regression lines: $y=28.69+0.440x$, $r^2=0.34$, $P<0.001$, $N=150$, and $y=24.67+0.576x$, $r^2=0.47$, $N=95$, for the Chhomrong and Dovan data, respectively.
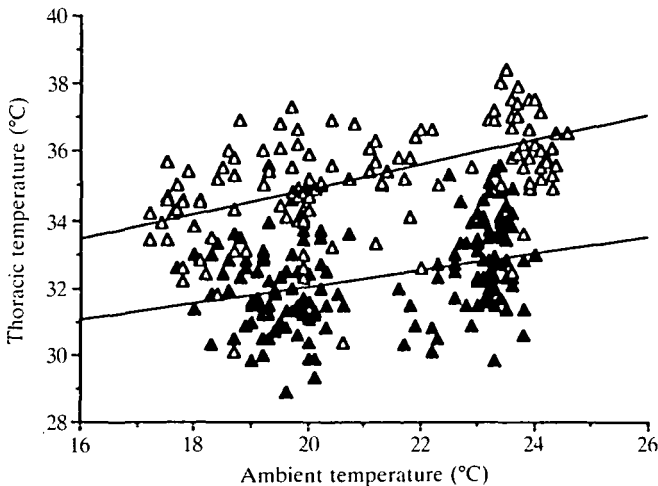

Fig. 3. Thoracic temperatures of *Apis dorsata* workers arriving in sunny weather at feeders offering concentrated (40–48%; △) or dilute (6–9%; ▲) sugar syrup. Regression lines: $y=27.65+0.359x$, $r^2=0.27$, $P<0.001$, $N=133$, and $y=27.13+0.245x$, $r^2=0.12$, $P<0.001$, $N=162$, for concentrated and dilute data, respectively.
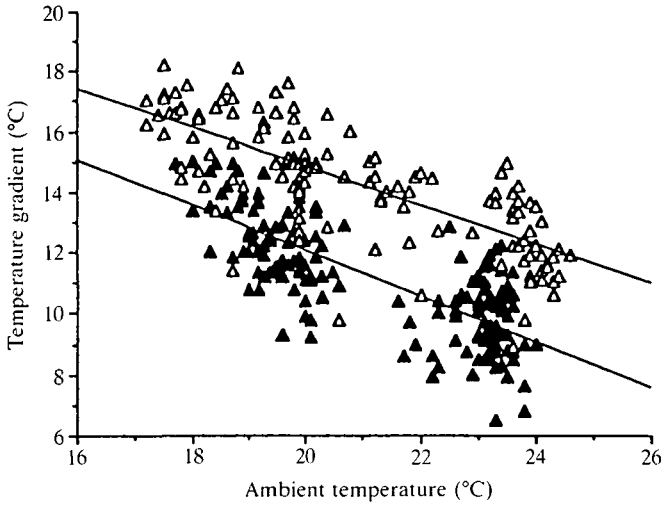
Fig. 4. Thoracic temperature gradients (difference between thoracic and ambient temperatures; transposed data from Fig. 3) maintained by *Apis dorsata* workers arriving to collect concentrated ($\triangle$) and dilute ($\blacktriangle$) sugar syrup. Regression lines: $y=27.65-0.641x$, $r^2=0.55$, $P<0.001$, $N=133$, and $y=27.13-0.755x$, $r^2=0.57$, $N=162$, for concentrated and dilute data, respectively.

Table 2. *Thoracic temperature gradients of* Apis dorsata *workers arriving on a single day at feeders varying in richness of syrup and degree of congestion*

Syrup concentration	Number of bees at feeder	Mean T_a	Mean $T_{th}-T_a$
17 % ($N=20$)	>60	23.8	10.0 ± 1.20^a
17 % ($N=19$)	≤16	24.2	10.5 ± 1.19^a
47 % ($N=24$)	<30	24.0	11.7 ± 1.00^b

All temperatures in °C; T_a, ambient temperature; T_{th}, thoracic temperature.
Numbers followed by different letters differ significantly ($P<0.001$, t-tests).
Values of the $T_{th}-T_a$ are mean±S.D.

arriving under sunny skies (Table 3). There was no observable effect of weather conditions on $T_{th}-T_a$ for bees arriving to collect dilute syrup at $T_a=20.5$°C.

In retrospect, the acclimation period of 20 min following a switch in syrup concentration at the feeders in Rampur was probably too short. Often, the only overlap in data collected before and after such a switch occurred within the first few (<10) bees tested following a change. Possibly these bees were still 'expecting' to collect a syrup of the previous concentration. This source of error could explain, in part, the very low correlation coefficients for the regression lines in Fig. 3. In other words, the true difference in $T_{th}-T_a$ between bees collecting concentrated and dilute syrups may have been even greater than that estimated here.

Table 3. *Thoracic temperature gradients of* Apis dorsata *workers arriving at feeders during sunny or overcast conditions*

Syrup concentration	Mean T_a (range)	Mean $T_{th} - T_a$		P
		Sunny	Overcast	
≥40%	19.3 (18.0–19.9)	15.2±1.51 $N=47$	14.1±1.50 $N=66$	<0.001
≥40%	20.8 (20.0–21.9)	14.3±1.35 $N=27$	12.8±1.26 $N=68$	<0.001
17%	20.5 (19.9–20.9)	11.6±1.41 $N=21$	11.3±1.17 $N=25$	NS

All temperatures in °C; T_a, ambient temperature; T_{th}, thoracic temperature; NS, not significant.
Values of $T_{th} - T_a$ are mean±S.D.

Table 4. *Thoracic temperature gradients of intact and depilated workers of* Apis dorsata *and* A. laboriosa *arriving at a feeder or about to take off*

Sample bees	N	Mean T_a	Mean $T_{th} - T_a$		P
			Intact	Depilated	
A. laboriosa arriving	16	15.5	19.6±1.23	17.3±1.61	<0.001
A. laboriosa taking off	19	17.6	19.2±1.25	19.2±1.09	0.806
A. dorsata arriving	9	21.6	11.7±2.86	9.3±2.47	<0.001

All temperatures in °C; T_a, ambient temperature; T_{th}, thoracic temperature.
Values of $T_{th} - T_a$ are mean±S.D.

Value of thoracic hairs to bees in flight

Table 4 presents data comparing the $T_{th} - T_a$ of intact and depilated workers of both *A. laboriosa* and *A. dorsata*. For both species, depilated workers arriving to collect syrup at a feeder had significantly lower gradients than intact bees. The difference in mean $T_{th} - T_a$ between intact and depilated bees was nearly identical for both species (2.3 and 2.4°C for *A. laboriosa* and *A. dorsata*, respectively). There was no difference in $T_{th} - T_a$ between intact and depilated *A. laboriosa* workers preparing to take off after imbibing syrup (time constraints did not permit a similar investigation with *A. dorsata*). Thus, the differences observed in arriving bees are probably attributable to the effects of the loss of insulating hair rather than to damage to the bees through handling.

Cooling curve

The cooling curve for a representative *A. laboriosa* worker is presented in
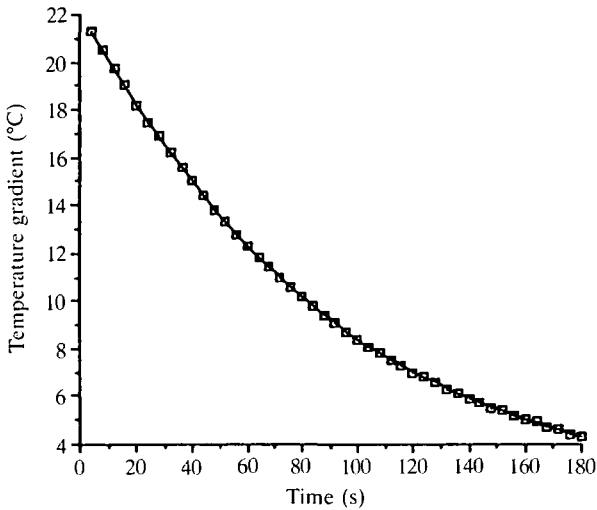
Fig. 5. Cooling curve of a typical *Apis laboriosa* worker. The temperature gradient is the difference between thoracic temperature and ambient temperature.

Fig. 5. If the logarithm of $T_{th} - T_a$ is plotted against time, the data describe a straight line, the slope of which (in s^{-1}) is the cooling constant (see Dyer and Seeley, 1987). For intact *A. laboriosa* workers, the cooling constant was $0.0042 \pm 0.0003\,s^{-1}$ ($N=15$), while for depilated bees ($N=8$) it was $0.0047 \pm 0.0002\,s^{-1}$ ($P<0.001$, t-test). The value for intact workers is slightly higher than the $0.0038\,s^{-1}$ that would be predicted on the basis of the thoracic mass of *A. laboriosa* by the regression ($y=0.0000421x^{-0.467}$) calculated by Dyer and Seeley (1987) for three other Asian species of *Apis*. It is, however, qualitatively as would be expected and the predicted cooling constant lies within the range of values provided by the several *A. laboriosa* cooling curves.

The difference between the cooling constants of intact and depilated *A. laboriosa* workers was only $0.0005\,s^{-1}$, about half that measured by Dyer and Seeley (1987) for *A. dorsata* workers. Possibly some of the *A. laboriosa* workers tested did not have a full complement of thoracic hairs initially, perhaps because they had been rubbed off during the long trip to Kathmandu. If this were the case, it would tend to increase the cooling rate of 'intact' bees, while decreasing the differences seen between intact and depilated workers. Such a problem would lead to a slight overestimation of the cooling constant, a slight overestimation of the actual cooling rate and a consequent overestimation of heat production in *A. laboriosa*, but correcting the problem would tend to strengthen, rather than to weaken, the arguments to follow.

Wing-loading

Wing-loading is correlated with power output (Casey, 1976) and has been found to be a very good predictor of flight temperature, especially in honeybees (see Dyer and Seeley, 1987). Wing-loading for *A. laboriosa* workers was calculated to

be $14.51 \, \text{N m}^{-2}$ (Table 1). Using this value in the equation $(y=0.1224x^{1.791})$ calculated by Dyer and Seeley for four other honeybee species yields a prediction that the $T_{th}-T_a$ of *A. laboriosa* in flight at $T_a=25\,°\text{C}$ should be about $14.7\,°\text{C}$. This is very close to the $T_{th}-T_a$ of $15.3\,°\text{C}$ (see Discussion for the efficacy of using this figure rather than data from Dovan) measured for workers returning to a swarm at $T_a=19.2\,°\text{C}$ and may be no different when it is considered that temperature gradients were found to be inversely related to T_a (i.e. *A. laboriosa*'s $T_{th}-T_a$ might be lower than $15.3\,°\text{C}$ at $T_a=25\,°\text{C}$).

The quotient of wing-loading and the cube root of body mass has been shown to yield a constant of about 250 for many species of flies and bees (Lighthill, 1978). Dyer and Seeley (1987) found that the values for both *A. florea* and *A. dorsata* were much closer to 250 than those of *A. cerana* and *A. mellifera*. The calculated value for *A. laboriosa* is 264.3, very close to the value obtained by Dyer and Seeley for *A. dorsata* and much lower than the values for the cavity-nesting species (see Table 1).

Dissections of the circulatory system

Dissections of the circulatory system of *A. laboriosa* workers (as well as workers of *A. dorsata* and *A. mellifera* for comparison) revealed no obvious differences from the reported morphologies of other species (Snodgrass, 1956; Dyer and Seeley, 1987). The aorta overlies the crop and esophagus and makes a series of 8–10 loops as it passes from the abdomen through the petiole. Heinrich (1980b) suggested that these loops might serve a heat-exchange function, prolonging the movement of relatively cool hemolymph from the abdomen into the thorax and allowing it to be heated by warmer hemolymph flowing in the opposite direction, thereby conserving heat in the thorax. The relatively low $T_{th}-T_a$ (in relation to the size of the bees) maintained by *A. laboriosa* workers in flight is probably not attributable to a relatively less efficient system for retaining heat in the thorax.

Discussion

The phenomenon of endothermy in flying insects has been regarded as 'simply a consequence of flight metabolism' (Heinrich, 1981). Heat produced in the flight muscles raises the insect's body (thoracic) temperature above ambient until a balance is struck between the rates of heat production and heat loss. Regulation of T_{th} could be accomplished by varying either or both of these rates.

Some insects have been shown to regulate T_{th} in flight by varying the rate of heat loss from the thorax. Certain moths (Heinrich, 1971; Casey, 1976) and bumblebees (Heinrich, 1975, 1976), among others, accomplish this by controlling the rate of exchange of hemolymph between the thorax and abdomen. Honeybees are apparently constrained by the morphology of their circulatory systems from using this method to cool the thorax (Heinrich, 1980b). Instead, *Apis mellifera* workers (and presumably those of other *Apis* species) can indirectly lower T_{th} at high T_a by evaporating water from droplets held in the mouthparts while in flight (Heinrich, 1980a).

Heinrich (1979) found that *A. mellifera* workers in a flight chamber maintained a relatively constant $T_{th} - T_a$ of 15 °C over a range of T_a from 15 to 25 °C. Heinrich (1980b) also reported that *A. mellifera* workers in a respirometer did not have a significantly different metabolic rate when flying at $T_a = 20$ °C than when in flight at $T_a = 42$ °C. He concluded that honeybees 'make no adjustment of heat production to stabilize T_{th} during flight'. Honeybees in the field seem to perform quite differently from those in the laboratory, however.

Heinrich's (1979) own data for *A. mellifera* workers during hive exits, foraging, attack and returns to the hive indicated thermoregulation at $T_a = 7-25$ °C. He suggested that this might have been accomplished by behavioral means (by bees alternately stopping to warm up and then flying again) or because the flights had been of short duration. An alternative explanation is that the bees were varying heat production while in flight at low T_a.

Schmaranzer and Stabentheiner (1988) found that *A. mellifera* workers arriving at a feeder offering a 0.5 mol l^{-1} sucrose solution had higher T_{th} than bees arriving to collect 0.25 mol l^{-1} syrup at another feeder an equal distance from the hive. They concluded that the bees remembered the quality of the food at a given feeder and that the differences in T_{th} reflected 'different stages of anticipation' on the part of the bees. Similarly, Dyer and Seeley (1987) reported that *A. cerana* workers arriving to collect concentrated syrup maintained higher $T_{th} - T_a$ than those arriving to collect more dilute syrup.

Data from the present study also challenge the traditional view that metabolic rates of flying honeybees are governed by the minimum requirements of flight and that workers do not vary heat production in flight. In particular, that traditional view cannot explain why *Apis dorsata* workers arriving to collect concentrated syrup had $T_{th} - T_a$ several degrees higher than those arriving to collect dilute syrup (Fig. 4), why the temperature gradients of *A. cerana*, *A. dorsata* and *A. laboriosa* workers were inversely related to T_a (Figs 1-4), or why *A. laboriosa* workers arriving at a swarm in sunlight had $T_{th} - T_a$ much lower than those arriving at a feeder under cloudy skies (Fig. 1). These data and those of others cited above can be explained if honeybee workers have the ability to choose their flight efforts and thereby, at least partially, regulate thoracic temperature.

As Waddington (1985) has observed, "the results of a study can be easily misinterpreted if the animal's decision 'rules' or processes change with respect to a manipulated variable". The concept that individual honeybees can alter their flight performance according to anticipated gains is an important one with major implications for field studies of foraging energetics. This concept must be examined in some detail before the original question of how *A. laboriosa* fits into the pattern of high-powered cavity-nesters *versus* low-powered open-nesters can be addressed.

If honeybees have the ability to choose their flight efforts, on what basis are the choices made? What advantage accrues to a bee flying with an elevated T_{th} or, conversely, what advantage is there in flying with a somewhat lower T_{th}?

The floral resources utilized by honeybees are spatially and temporally

distributed such that a colony often experiences a boom or bust economy (see Seeley, 1985). Bees cannot predict in advance when a rich source of nectar might suddenly become available in close proximity to the nest. If a forager's objective is to maximize her lifetime contribution to the colony's energy budget, and if the degree of physiological activity affects her lifespan (Neukirch, 1982; Schmid-Hempel *et al.* 1985; Wolf and Schmid-Hempel, 1989), the best strategy for a bee gathering a marginal resource might be to work at a pace that ensures the longest (in terms of days) foraging career. Then, if a bonanza occurs, she might still be available to help the colony gather it, rather than having spent herself rushing to bring in the less profitable resource. But what if a particularly rich source of nectar does come into bloom? Then, it would make sense to attempt to exploit that resource to the fullest as quickly and efficiently as possible. If the quality of the food source is such that it is as good as or better than anything else the bees are likely to encounter, there would seem to be no advantage in holding back. Thus, if foragers consistently use the currency of energetic efficiency [(gain−cost)/cost; Schmid-Hempel *et al.* 1985] in making foraging decisions, a bee working a marginal patch might consider the cost of flight in terms of senescence, while one gathering a particularly rich resource might discount that cost or ignore it altogether.

The mechanical efficiency of an *A. mellifera* worker's flight system increases with increasing T_{th}, with changes in wingbeat frequency and lift being most dramatic up to $T_{th} \approx 33\,°C$ (Esch, 1976). Wingbeat frequency continues to increase (but at a slower rate) up to $T_{th} \approx 38\,°C$, while lift remains essentially constant. If there is an optimal temperature at which the flight muscles operate most efficiently, this must also enter into the decision-making process.

Actively increasing T_{th} within the range 33–38 °C may be associated with relatively greater costs (including senescence) that cannot be justified by bees working relatively poor resources. *A. dorsata* workers collecting dilute syrup maintained a minimum flight temperature of about 32–33 °C and apparently made little effort to keep T_{th} above that level. Thus, T_{th} of bees changed little over a 6° range of T_a (Fig. 3) and T_{th} of bees collecting 17 % syrup was no different in sunny weather from that under overcast skies (Table 3).

The needs of a colony at a particular time must also enter into the decision-making process (Seeley, 1986, 1989). If, for instance, a colony is on the verge of starvation when a resource that ordinarily would be considered marginal becomes available, it might be appropriate for the foragers to treat that resource as they would a particularly rich one.

If bees are able to choose their flight effort and if many variables enter into that choice, is it hopeless to attempt to make interspecific comparisons based on the thoracic temperature gradient maintained by workers in flight? Dyer and Seeley (1987) gathered the bulk of their data on *A. cerana*, *A. dorsata* and *A. florea* at feeders offering relatively dilute sugar syrup during sunny weather at ambient temperatures of about 24–32°C. In the present study, $T_{th} - T_a$ of *A. dorsata* workers arriving in sunny weather to collect dilute (6–9 %) sugar solution was

measured at a range of T_a of about 18–24°C. For these workers, $T_{th} - T_a$ ranged from about 9–14°C and was inversely related to T_a (Fig. 4). The gradient of 9° at a T_a of about 24°C is within the range of 9–12°C reported by Dyer and Seeley (1987) for *A. dorsata* in Thailand. Thus, there is some indication that the methods used in the two studies produced comparable results and that these may allow meaningful comparisons to be made between the data sets.

Flight temperatures of *A. cerana* in Nepal were considerably higher than those measured by Dyer and Seeley (1987) for *A. cerana* in Thailand. At congested feeders (offering relatively concentrated syrup) in Thailand, *A. cerana* workers flew with $T_{th} - T_a \approx 16$°C at $T_a \approx 23$°C, while in Nepal, *A. cerana* arriving to collect concentrated syrup flew with $T_{th} - T_a \approx 19$°C at $T_a \approx 18$°C (Fig. 2). The difference in $T_{th} - T_a$ may be attributable to the much larger size of *A. cerana* in Nepal.

Temperature data for *A. cerana* and *A. dorsata* in Nepal (see Table 1) support the pattern of high-powered cavity-nesters *versus* low-powered open-nesters discovered by Dyer and Seeley (1987). Where does *A. laboriosa* fit into that pattern? In overall body plan, *A. laboriosa* workers seem to be scaled-up versions of the other honeybee species, without other obvious adaptations. The thorax is of a size appropriate to the overall body mass (Table 1) and the circulatory system apparently differs little from that of other honeybees. *Apis laboriosa* workers do have much longer body hairs than *A. dorsata* workers (thoracic hairs are more than 30% longer; Sakagami *et al.* 1980), but the relative effectiveness of this insulation is questionable. The cooling constant for *A. laboriosa* is lower than that of *A. dorsata*, but shaving experiments suggest that this is probably the result of the larger body size of the former, rather than an indication of the quality of the insulation provided by body hairs.

Of central importance to the question of how *A. laboriosa* compares in energetic traits to other species of *Apis* is a determination of the $T_{th} - T_a$ maintained in flight. For comparison with the data of Dyer and Seeley (1987), it would be desirable to have data gathered from *A. laboriosa* workers arriving to collect dilute (relatively unattractive) syrup in sunlight. The data from bees arriving to collect concentrated syrup under overcast skies at Dovan (Fig. 1) are clearly inappropriate. Fortunately, the limited data from bees arriving at a winter cluster in sunny weather (Fig. 1) are probably useful. Since these data were gathered on the day the swarm moved from its winter quarters to a cliff site a few hundred meters away (see Underwood, 1990), and since the bees all had empty honey stomachs, these *A. laboriosa* workers were probably scouts returning from a search for a home site. The mean $T_{th} - T_a$ of these bees was 15.3°C at $T_a = 19.2$°C.

If 15.3°C is approximately the $T_{th} - T_a$ of an *A. laboriosa* worker with minimal expected energetic gain, this value may be used for comparison with values obtained for workers of other species of *Apis* in other studies. A gradient of 15.3°C is essentially the same as the 15°C reported by Heinrich (1979) for *A. mellifera*, a bee with only half the body mass of *A. laboriosa*. The bees tested by Heinrich were flown in a flight chamber and so must also have had a minimal expected gain; their temperature gradients were lower than those maintained by

A. cerana workers collecting concentrated syrup in Nepal (Fig. 2). Since *A. laboriosa* is a much larger bee than *A. mellifera* and therefore cools more slowly (there is no reason to believe that *A. laboriosa* would enhance its cooling rate at the range of ambient temperatures observed), it follows that *A. laboriosa* workers must have had a lower rate of heat production.

Both the thoracic temperature gradient and the calculations of $mass^{1/3}$-specific wing-loading suggest that *A. laboriosa* may be grouped with *A. florea* and *A. dorsata* as a relatively low-powered honeybee. This lends credence to the idea that, in honeybees, an open-nesting lifestyle places certain constraints on worker physiology (Dyer and Seeley, 1990).

The large size of *A. laboriosa* workers is almost certainly one of the major adaptations that has enabled this species to survive in temperate climates while the other open-nesting honeybees are confined to the tropics and subtropics. *A. laboriosa* workers are able to forage at ambient temperatures at least 5–6 °C lower than the minimum T_a at which *A. dorsata* workers can fly (this study and Dyer and Seeley, 1987). This has apparently been accomplished largely through an increase in body size, without resort to creating a higher-powered bee and without a disproportionate increase in thoracic mass, such as seems to have been the case with *A. cerana* in Nepal.

The above discussion has been an attempt to reconcile the data obtained in the present study with those reported previously about the energetics of flying honeybees. While the original question of how *A. laboriosa* fits into the pattern observed by Dyer and Seeley (1987) has been answered to some degree, many more questions have been raised. It has been argued that honeybees seem to be able to adjust their flight efforts in accordance with expected gains from foraging bouts and to compensate, at least partially, for lower ambient temperatures. Since this conclusion was based largely on the flight temperatures of honeybees arriving at feeders, it may have limited validity for bees foraging in nature. Perhaps bees flying from flower to flower, obtaining a small fraction of a load at each, must budget themselves differently from bees that 'know' they can fill their crops at a feeder.

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