

Hot bumble bees at good food: thoracic temperature of feeding *Bombus wilmattae* foragers is tuned to sugar concentration

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Summary

The ability of bees to generate metabolic heat plays an important role in their ability to forage and pollinate because they must achieve a minimum temperature to activate their flight muscles. In honey bees and stingless bees, the thoracic temperature of feeding foragers is correlated with the caloric value of sucrose solution provided at feeders outside the nest. We provide the first detailed data showing that this phenomenon also occurs in the closely related bumble bee and thus may be homologous in all social bees of the Apidae. Using infrared thermography, we measured T_{th} for *Bombus wilmattae* foragers (mass 0.17 ± 0.11 g, length 15.0 ± 1.5 mm) from six wild colonies, foraging on a range of sucrose

concentrations (0.5–2.5 mol l⁻¹, 16–65% by mass) in foraging arenas. For all colonies, we measured significant increases in ΔT_{th} ($P < 0.0001$) with increasing sucrose concentration, with significant differences ($P < 0.0001$) between colonies due to different linear regression slopes (0.28–2.4) and y-intercepts (2.7–5.5). We suggest that this modulation of pitching T_{th} to sucrose concentration is a general phenomenon in all social bees and may be a widespread adaptation facilitating rapid food collection in flying Hymenoptera.

Key words: thermoregulation, foraging, food quality, endothermy, *Bombus*.

Introduction

The modulation of body temperature by active or passive means at or near a specific set point is found widely among insects (Heinrich, 1993), particularly in the Hymenoptera (Himmer, 1932). Researchers have reported thermoregulation in ants (Hölldobler and Wilson, 1990), wasps (Stabentheiner et al., 2004), solitary bees [Anthophora (Stone, 1994)] and social bees (Bujok et al., 2002; Dyer and Seeley, 1987; Kleinhenz et al., 2003; Stabentheiner et al., 1990; Stone and Willmer, 1989). Here, we focus on the phenomenon of thoracic metabolic heat production linked to food quality.

Flight thermoregulation is widely found among bees (Stone and Willmer, 1989), including solitary bees [*Xylocopa virginica* (Baird, 1986)]. All bees in which thermoregulation has been examined are heterotherms (Heinrich, 1993) and can regulate higher body temperatures during foraging and attacks (Heinrich, 1979). Thermoregulation plays a role in the ability of bees to fly (Coelho, 1991; Esch, 1976) and thus to visit flowers under cold conditions (Corbet et al., 1993). *Bombus terrestris*, *B. pascuorum* and *B. hortorum* began foraging at lower temperatures than honey bees and were thus expected to forage earlier in the morning and later in the afternoon than honey bees (Corbet et al., 1993), a potential example of how

thermoregulation allows niche specialization. Recently, bumble bees (*B. terrestris*) have also been shown to be able to associate warmth with floral color, preferring to visit warmer flowers in a flight arena (Dyer et al., 2006).

Several species of honey bees, including *Apis mellifera*, *A. cerana*, *A. dorsata* and *A. laboriosa*, are able to regulate their body temperature, exhibiting higher thoracic temperatures after feeding at rich sucrose solutions than at poorer sucrose solutions (Schmaranzer and Stabentheiner, 1988; Underwood, 1991). In general, honey bee thoracic temperature corresponds to the quality of the food source as perceived by sweetness (Stabentheiner and Hagmüller, 1991), proximity to the nest (Esch, 1960; Stabentheiner, 1996) and nectar flow rate (Farina and Wainselboim, 2001), with increasing net caloric intake per unit time giving rise to higher temperatures. In honey bees, metabolic expenditure increases with increasing nectar flow rate at an artificial feeder (Balderrama et al., 1992; Moffatt and Nunez, 1997). On a feeder, honey bees evidently traded off the amount of energy expended in keeping the thorax warm and thus in a state of immediate readiness for takeoff (Moffatt, 2001) versus net caloric benefits to the colony by expending less energy in thoracic heating for poorer food (Waddington, 1990). Honey bees are thus able to adjust their energetic

expenditure and exploit relatively poor food when richer food is not readily available.

Recently, foragers of the stingless bee *Melipona panamica* (Meliponini) also have been shown to adjust their thoracic temperature according to food caloric value. Like honey bees, *M. panamica* foragers maintained a thoracic temperature T_{th} excess above air temperature T_a (21.5–29.5°C) that corresponded to sucrose concentration when unloading food and recruiting nestmates inside the nest (Nieh and Sánchez, 2005). Thus the phenomenon of increasing thoracic temperature with increasing sucrose concentration may be common among the flying Hymenoptera.

Bumble bees

In their study of bumble bee field foraging, Heinrich and Heinrich observed an interesting phenomenon in *B. vagans*, *B. terricola* and *B. perplexus* foragers and wrote: (p. 561) “flight activity by itself cannot account for the high T_{th} (>34°C) observed on raspberry, since bees often perched on flowers and resumed flight fully heated; they maintained an elevated T_{th} even while they were perched” (Heinrich and Heinrich, 1983b). Based upon recent findings that stingless bee foragers (Meliponini, *Melipona panamica*) can maintain elevated T_{th} temperatures tuned to food caloric concentration while feeding (Nieh and Sánchez, 2005), and given that honey bees (Apini) do the same (Stabentheiner, 2001; Stabentheiner and Haggmüller, 1991), we examined whether their close relatives, the bumble bees (Bombini), possess a similar ability.

Bombus wilmattae (Cockerell, 1912) is restricted in distribution to the highlands of Chiapas and Guatemala, corresponding to that of the Bosque de Pino y Encino and the Bosque Tropical Caducifolio (Labougle, 1990; Rzedowski, 1978). Elevational distribution of this species, based upon this and additional studies in preparation (21 additional colonies, R.V., unpublished) is between 1413 m and 2014 m. This is considered a tropical-to-subtropical species, which makes our study particularly interesting because examinations of bumble bee thoracic temperature have largely been restricted to temperate species.

Materials and methods

Study site and colonies

We collected six wild colonies of *Bombus wilmattae* (Cockerell, 1912) around the towns of Unión Juárez, Talquian, and San José, in Chiapas, Mexico at altitudes ranging from 1110 to 1690 m (laboratory designations: BW5, BW8, BW10, BW12, BW13 and BW14). We used BW5 from November to December 2003 and other colonies from August to September 2005. Colonies were transferred to wood observation hives (30 cm×30 cm×30 cm for colony BW5 and 18 cm×18 cm×18 cm for all other colonies) covered with glass. Experiments were conducted inside a laboratory at El Colegio de la Frontera Sur, Tapachula, Chiapas, Mexico (14°53.191'N, 92°17.183'W) inside wood foraging arenas (120 cm×90 cm×30 cm, L×W×H) covered with IR

transparent plastic film [BCU Plastics, Polyolefin FDA grade 75 gauge film, catalog #LS-2475, protocol of Stabentheiner and Haggmüller (Stabentheiner and Haggmüller, 1991)]. Each colony was connected to a single, separate foraging arena through a 3.5 cm diameter, 10 cm long, clear vinyl tube. All colonies were maintained inside the laboratory for at least 20 days before use in the experiments and provided *ad libitum* with 50% (v/v) honey/water. All trials were conducted inside a light and temperature-controlled room (24.4±1.9°C). We visually inspected the exposed honey pots of each colony before using them in experiments and found that the food stores (honey and pollen) of all colonies were similar.

Feeders and censusing

Before beginning our experiments, we used paired feeders for a preliminary test of any potential sucrose concentration effect, and a resulting thermographic image is shown to better illustrate the effect of sucrose concentration on forager body temperatures. In our experiments, we measured the temperatures of bees foraging at a single feeder containing unscented 0.5, 1.0, 1.5, 2.0 or 2.5 mol l⁻¹ sucrose solutions (double distilled water and reagent grade sucrose, Quimica Meyer, cat#6710-1000, Tapachula, Mexico). Beginning at 09:00 h on each experimental day, we presented the colony with a single sucrose concentration for 30 min, followed by a 5 min pause (when no sucrose was available) before providing the next sucrose concentration. We presented all five concentrations on each day, alternating between ascending and descending concentration series on subsequent experimental days. We thoroughly cleaned the feeder between concentration changes. Each colony was used for two complete concentration series and thus experienced both diminishing and increasing sucrose concentrations.

Foragers were individually marked either with Opalithplättchen honey bee tags (colony BW5) or with small acrylic paint marks on their abdomens (all other colonies). Every 5 min, we made an instantaneous count of the number of foragers collecting sucrose solution at the feeder. Thus we made six counts during each 30 min presentation of a particular sucrose concentration. To examine the proportion of colony foraging elicited by different sucrose concentration, we calculated the normalized forager census count (F_N) by dividing the census count by the largest census count obtained for that colony at any sucrose concentration. We used a circular grooved plate feeder [40 ml capacity, 10 cm diameter, 60 grooves, design after description by von Frisch (von Frisch, 1967)]. Foragers fed *ad libitum* (feeder was never exhausted during the 30 min feeding trial), and the feeder did not limit forager numbers because each feeder could accommodate over 35 individuals; we observed a maximum of 25 foragers feeding simultaneously. To determine forager size, we randomly selected 15 live foragers from each colony, weighed them in plastic vials and measured their length (from abdominal tip to anterior head) with calipers. Colonies were not fed outside of the experimental period, but were not food deprived because

daily visual inspections revealed largely full honeypots in exposed areas of each colony.

Temperature measurements

We used infrared thermography to measure forager thoracic surface temperatures (Stabentheiner and Schmaranzer, 1987). We recorded bee temperatures 5 s after they had begun feeding on the feeder using a photographic infrared thermometer (Raytek PhotoTemp MX6, San Diego, CA, USA; close-focus model) equipped with True Spot laser sighting to precisely delineate the measured area (spot measurement size adjustable to the diameter of a bumble bee thorax). Each time we made a thermographic measurement, we measured air temperature 5 cm from the feeder (T_a) using a weather meter (Kestrel 3000, Chester, PA, USA). To calibrate the MX6 infrared thermometer, we inserted a type K thermocouple into a dead bee whose internal and external temperature had equilibrated to ambient, and then recorded its dorsal thoracic surface temperature through the IR transparent plastic film. Equipment emissivity values were then adjusted until both thermocouple and infrared temperature readings matched. We measured T_{th} and T_a , and calculated the difference between the thorax temperature and the ambient air temperature at the feeder [ΔT_{th} (Stone, 1993)].

Statistical analyses

We used JMP IN v4.0.4 software to run ANOVA (standard least-squares model) after checking for data normality through residual analysis (Zar, 1984). Models with multiple effects

were run first with all interaction terms and then run as simplified models without interactions if interactions were non-significant (Zar, 1984). Values are presented as means \pm s.d. We considered results non-significant (NS) at the critical value $P \geq 0.05$.

Results

Feeding behavior

The majority of foragers walked from the entrance of the foraging arena to the food source, although some bees flew briefly before landing near the feeder. At the conclusion of feeding, the majority of foragers walked back to the nest, but some took off and flew for a short period of time before landing and entering the nest. At all sucrose concentrations, foragers exhibited abdominal respiratory movements with the exception of seven evidently ectothermic foragers (Fig. 1), who fed at the lowest sucrose concentration offered (0.5 mol l^{-1}) and whose respiratory frequency was too low to be detected by eye. All foragers either folded their wings over their abdomens or, in some cases, performed wing buzzing in which the wings fluttered rapidly in an arc of $10\text{--}85^\circ$ relative to the body. On average, live foragers weighed $0.17 \pm 0.11 \text{ g}$ and were $15.0 \pm 1.5 \text{ mm}$ in length ($N=90$ total foragers, 15 randomly selected from each colony).

Effect of ambient air temperature

We first examined the effect of T_a on T_{th} at each sucrose concentration. In the overall model, both T_a and sucrose

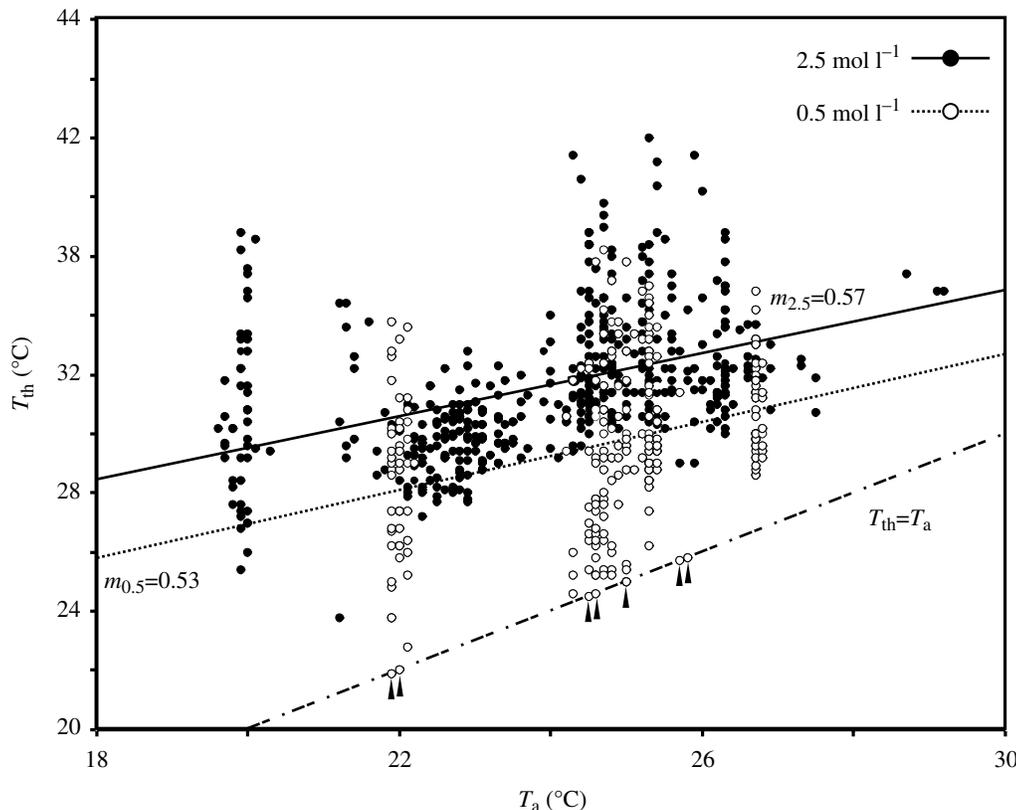


Fig. 1. Elevated thoracic temperatures of foragers feeding on sucrose solutions. The relationship between thorax temperature (T_{th}) and ambient air temperature (T_a) for feeding bees. With the exception of seven measurements from evidently ectothermic foragers at the lowest sucrose concentration (marked by black arrows), all T_{th} values are above T_a (lower broken line). Pooled data from all colonies for the highest and lowest sucrose concentrations (m) used are shown ($m=0.5 \text{ mol l}^{-1}$: $N_{colonies}=6$, $N_{measurements}=250$, $N_{individual \text{ bees}}=161$; $m=2.5 \text{ mol l}^{-1}$: $N_{colonies}=6$, $N_{measurements}=497$, $N_{individual \text{ bees}}=161$). Linear regression lines with y-intercept values are given.

Table 1. *Effect of sucrose concentration on forager thoracic temperature at the feeder*

Sucrose concentration		Temperature (°C)			Regression				
mol l ⁻¹	%	ΔT_{th}	T_{th}	T_a	T_{th} vs T_a	ANOVA	F_N (%)	N	
0.5	16	4.9±2.7	29.7±2.7	24.7±1.6	$y=15.5+0.57x$	$F_{1,248}=29.5, P<0.0001, R^2=0.11$	20.5±9.9	250	
1.0	31	5.5±2.5	29.6±2.8	24.2±2.4	$y=13.7+0.66x$	$F_{1,374}=165.1, P<0.0001, R^2=0.31$	35.1±13.5	376	
1.5	34	6.8±2.7	31.7±2.2	24.9±1.5	NS	$F_{1,248}=0.02, P=0.89, R^2<0.0001$	42.1±15.0	250	
2.0	41	7.3±2.7	32.0±2.2	24.7±1.4	NS	$F_{1,248}=2.3, P=0.13, R^2=0.009$	52.1±17.6	250	
2.5	65	7.7±2.3	31.6±2.4	23.9±1.9	$y=18.8+0.53x$	$F_{1,495}=114.6, P<0.0001, R^2=0.19$	61.0±21.4	497	

T_{th} , thoracic temperature; T_a , air temperature; F_N , normalized forager census count.

Values are means ± s.d.

Percentage sucrose concentration by mass (g sucrose 100 g⁻¹ solution) obtained from Bubnik et al. (Bubnik et al., 1995).

Although a significant colony effect was found for the relationship between ΔT_{th} and sucrose concentration, we provide the average values here as a simplified reference because inter-colony differences were fairly minor.

concentration are significant effects, but colony identity is not (two-factor ANOVA, $F_{2,1620}=243.0, P<0.0001$; individual effects: T_a , $F_{1,1620}=1484.4, P<0.0001$; sucrose concentration; $F_{1,1620}=1491.2, P<0.0001$; colony identity NS; interactions NS). We therefore pooled the data from all colonies and examined the relationship between T_{th} and T_a at each sucrose concentration. Foragers generally increased their thoracic temperature above ambient at all sucrose concentrations, and the slope of T_{th} on T_a is significantly less than one for all concentrations (slope confidence intervals: $P<0.001$). For clarity, Fig. 1 shows only the highest and lowest concentrations. Note that with only the exception of seven evidently ectothermic foragers (all at 0.5 mol l⁻¹), all other T_{th} values are higher than ambient air temperature (Fig. 1). These seven different bees (from colonies BW5, BW8 BW10, BW13 and BW14) also did not show any noticeable abdominal respiratory movements. On average, forager T_{th} increased by 0.53 to 0.66°C for each 1°C increase in ambient air temperature over the range of sucrose concentrations used.

Effect of sucrose concentration on thorax temperatures

We next examined the effect of sucrose concentration on ΔT_{th} (Table 1). The overall model for ΔT_{th} with sucrose concentration and colony identity is significant (two-factor ANOVA, $F_{6,1616}=152.2, P<0.0001, R^2=0.36$, interaction NS). Sucrose concentration is a significant effect ($F_{1,1616}=475.4, P<0.0001, SS_{sucrose}=2292.6$). Colony identity is also a significant effect ($F_{5,1616}=106.6, P<0.0001, SS_{colony}=2569.4$). A detailed analysis by colony reveals that ΔT_{th} significantly increases with sucrose concentration with all colonies, with linear regression slope estimates ranging from 1.2 to 2.4 (Table 2). Thus foragers increased their thoracic temperature excess, on average, by 1.2 to 2.4°C for each 1 mol l⁻¹ increase in sucrose concentration.

Effect of sucrose concentration on colony foraging

There is a significant effect of colony identity and sucrose concentration on F_N (the normalized forager census count, two-factor model ANOVA, $F_{6,1615}=241.4, P<0.0001$,

$R^2=0.47$, interaction NS). Colony identity is a significant effect ($F_{5,1615}=35.5, P<0.0001, SS_{colony}=4.5$). Sucrose concentration is also a significant effect ($F_{1,1615}=1082.2, P<0.0001, SS_{sucrose}=27.6$), and accounts for approximately six times more of the variance in F_N than colony identity. A detailed analysis by colony reveals that F_N significantly increased ($P<0.0001$) with sucrose concentration in each colony. Linear regression slope estimates for the colonies fell into two groups: those with slopes of 0.16–0.18 (colonies BW5, BW8, BW10 and BW14: group 1) and those with slopes of 0.21 and 0.23 (colonies BW12 and BW13: group 2). We therefore present these data pooled into two groups (Fig. 2C), with sucrose concentration accounting for 40% of the variance in F_N of group 1 (ANOVA $F_{1,1120}=739.1, P<0.0001$) and 46% of the variance in F_N of group 2 (ANOVA: $F_{1,498}=424.5, P<0.0001$). On average, the proportion of feeding foragers increased by 18% with each 1 mol l⁻¹ increase in sucrose concentration in group 1 and by 22% with each 1 mol l⁻¹ increase in group 2.

Discussion

Bombus wilmattae foragers from six different wild colonies consistently increased their thoracic temperatures when feeding at food with higher carbohydrate rewards (Figs 1 and 2). For each colony, F_N also increased with increased sucrose concentration (Fig. 2C). Although colony effects were found for ΔT_{th} , each colony exhibited the same trends of increasing ΔT_{th} and increasing F_N with increasing sucrose concentration (Table 2). Thus the phenomenon of increasing thoracic temperature of foragers feeding while stationary upon food with increasing caloric value has now been shown to occur in the Bombini and may be homologous in all social bees in the Apidae.

A low T_{th} may be costly because it increases the time between exploiting different inflorescences by prolonging pre-flight warm-up or increasing escape times when avoiding predators. With a variety of bumble bee species and worker sizes, a T_{th} of approximately 29–30°C is required for flight

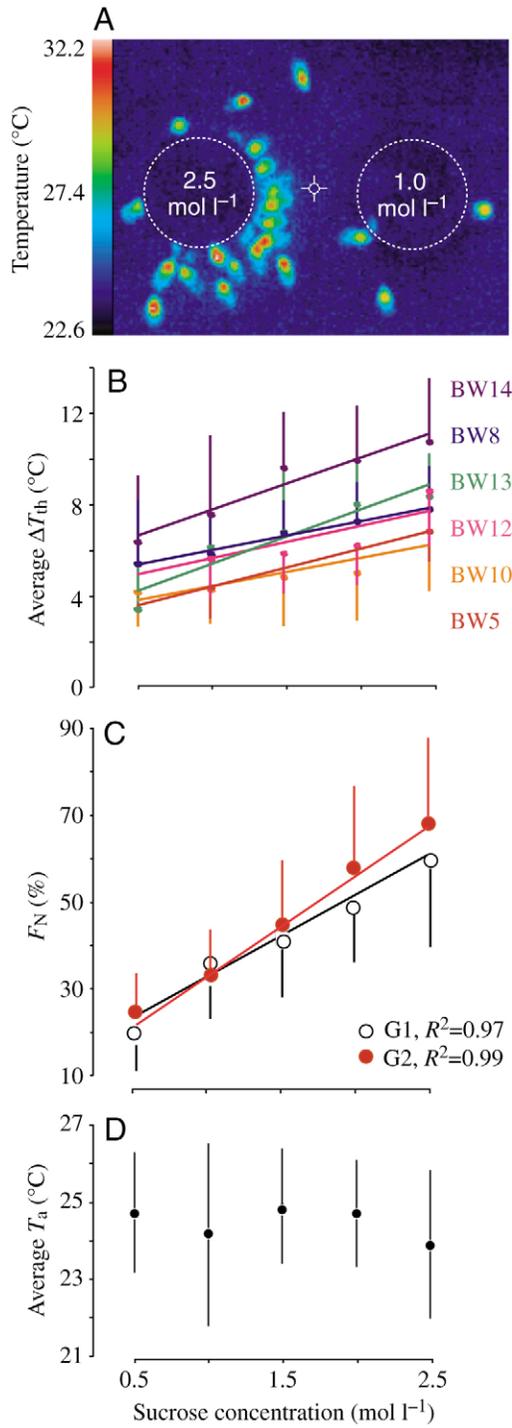


Fig. 2. Effect of sucrose concentration on (A) forager body temperature as shown through a thermal image (Raytek ThermoView Ti30 infrared imager, FLW Inc., San Diego, CA, USA) during a preliminary investigation of colony 1 on sucrose concentrations of 1 mol l⁻¹ or 2.5 mol l⁻¹, (B) average ΔT_{th} , (C) proportion of foragers adjusted for different colony sizes (G1 and G2 refer to colonies groups 1 and 2, respectively; see text). (D) Average ambient air temperatures T_a during the trials are also shown. Values are means \pm 1 s.d.

Table 2. Colony information and colony effects on the relationship between ΔT_{th} and sucrose concentration and between the normalized census count of foragers and sucrose concentration

Colony		ID	N_{colony}^a	Collection date	Location	Altitude (m)	$N_{experiment}$	ΔT_{th} vs [sucrose] ^b	N_{max} foragers	F_N vs [sucrose] ^b
		BW5	98	8 November 2003	Unión Juárez 15°05.25'N, 92°05.28'W	1572	52	$F_{1,351}=265.5, P<0.0001, R^2=0.43, y=2.7, slope=1.6$	25	$F_{1,351}=150.2, P<0.0001, R^2=0.30, y=0.24, slope=0.16$
		BW8	61	24 March 2005	America 15°03.95'N, 92°04.94'W	1223	21	$F_{1,248}=47.8, P<0.0001, R^2=0.16, y=4.7, slope=1.2$	9	$F_{1,248}=160.5, P<0.0001, R^2=0.39, y=0.21, slope=0.17$
		BW10	53	27 April 2005	Chiquihuites 15°05.83'N, 92°06.19'W	2014	25	$F_{1,250}=45.2, P<0.0001, R^2=0.15, y=3.2, slope=1.2$	9	$F_{1,250}=186.4, P<0.0001, R^2=0.43, y=0.16, slope=0.17$
		BW12	41	4 May 2005	Talquian 15°05.55'N, 92°05.71'W	1676	14	$F_{1,248}=60.0, P<0.0001, R^2=0.19, y=4.2, slope=1.4$	6	$F_{1,248}=226.2, P<0.0001, R^2=0.48, y=0.13, slope=0.23$
		BW13	62	4 May 2005	Talquian 16°05.53'N, 92°05.72'W	1675	22	$F_{1,247}=96.3, P<0.0001, R^2=0.28, y=3.0, slope=2.4$	9	$F_{1,247}=236.9, P<0.0001, R^2=0.49, y=0.07, slope=0.21$
		BW14	65	25 May 2005	Talquian 15°05.36'N, 92°05.98'W	1690	27	$F_{1,266}=81.4, P<0.0001, R^2=0.23, y=5.5, slope=2.2$	11	$F_{1,266}=165.7, P<0.0001, R^2=0.38, y=0.06, slope=0.18$

^aTotal number of bees in each colony counted at the time of the experiments.

^bLinear regression values.

$N_{experiment}$, number of foragers used in experiment; N_{max} foragers, maximum number of foragers simultaneously at feeder.

(Heinrich, 1974). So maintaining a high T_{th} , and thus flight readiness, may allow workers to gamble on the chance of finding a new food source (Heinrich and Heinrich, 1983a). For food of lower quality, less energy could be spent on maintaining higher thoracic temperature to optimize net caloric returns to the colony (Stabentheiner et al., 1995). Body temperature decreases when foraging on relatively poor quality food could have evolved in bumble bees as an energy-conserving strategy under active physiological control or perhaps to a lack of direct energy supplies (Heinrich and Heinrich, 1983a), although in honeybees there is no correlation between haemolymph sugar levels and body temperatures, except for a slight effect with highly dilute sucrose solution (Blatt and Roces, 2001; Blatt and Roces, 2002). High T_{th} may also be adaptive on natural food sources to properly harvest the food, particularly pollen (Feuerbacher et al., 2003). For example, *B. terricola* workers may have maintained a high T_{th} to collect pollen by twirling around *Spiraea latifolia* inflorescences (Heinrich and Heinrich, 1983a).

Colonies were of different sizes and were collected at different times of year and thus potentially at different life stages (S.C., unpublished observations). Both of these effects may account for differences in the proportion of workers activated to forage at given sucrose concentrations, in addition to differences in colony food stores. We found colony differences in slope and y-intercept for the effect of sucrose concentration on ΔT_{th} and F_N , although in all cases, there was a significant positive effect of sucrose concentration on ΔT_{th} and F_N (Table 2). In particular, our largest colony, BW5, exhibited the strongest correlations between sucrose concentrations and ΔT_{th} ($R^2=0.43$). We speculate that worker thresholds for sucrose collection and thus the perceived quality of different sucrose concentrations may also have varied with either colony stage (whether the colony was at the beginning of its life cycle and growing or near the end of its life cycle and collecting relatively little food) or food stores. With our current data, we are unable to determine whether seasonality and colony life stage play a role in finely modulating the effects of sucrose concentration on ΔT_{th} and F_N , although this would be important to test in future studies.

It is relevant to consider how our experimental design may have affected our measurements. Floral nectars occur at a variety of sugar concentrations (Baker and Baker, 1982) and generalist neotropical bee foragers collect nectars ranging from 10%–70% sugar by mass [with means of 38%, 44% and 48% for Euglossini, Meliponini and Centridini, respectively (Roubik et al., 1995)]. We therefore used sucrose concentrations ranging from 0.5–2.5 mol l⁻¹ (16% to 65% by mass), with the highest sucrose concentration (2.5 mol l⁻¹) used to provide comparative data with foraging studies on other social bees.

We conducted our experiments with colonies foraging in foraging arenas, a standard experimental design for investigations of bumble bee foraging (Chittka et al., 2003; Dornhaus and Cameron, 2003; Dornhaus and Chittka, 1999; Dornhaus and Chittka, 2004; Dyer et al., 2006; Spaethe et al., 2001). In most cases, bumble bees walked to the food source,

but some flew and we did not detect any differences between the T_{th} effect of sucrose concentration on bees that had walked or flown to the food source. Nonetheless, it would be desirable to verify the effect of sucrose concentration on T_{th} with flying bees using a large flight arena.

In *B. wilmattae* the average ΔT_{th} increased by 4.2°C with each 1 mol l⁻¹ increase in sucrose concentration. This is a greater increase than is found in honey bees [1.5°C increase in thoracic temperature per doubling of the sucrose concentration (Schmaranzer and Stabentheiner, 1988)]. Foragers of the stingless bee *M. panamica* increased T_{th} by 0.9°C per 1 mol l⁻¹ increase in sucrose concentration (Nieh and Sánchez, 2005). Body size may play a role in the effect of sucrose concentration on T_{th} excess, because the bumble bee foragers that we studied are larger than honey bees, which are in turn larger than *M. panamica*. This may be an interesting question to pursue in future comparative studies within and between bee groups.

In our study, the tropical species, *B. wilmattae*, maintained thoracic temperatures on average between 29°C and 32°C while foraging, similar to the range reported by Heinrich and Heinrich in a study of temperate *Bombus terricola* foraging on field spiraea (*Spiraea latifolia*) and goldenrods (*Solidago* sp.) (Heinrich and Heinrich, 1983a). Because there have been no similar studies on the effect of sucrose concentration on temperate bumble bees foraging while perched, future investigations may look for differences between the T_{th} and ΔT_{th} of tropical and temperate bumble bees flying to food sources. For example, at 2.5 mol l⁻¹, we found an average T_{th} of 31.6°C at an average T_a of 24.7°C. Studies conducted under similar ambient temperatures and sucrose concentrations will be necessary to draw conclusions on potential differences or similarities between tropical and temperate bumble bees.

The forager abdominal pumping movements that we observed during our experiments are common in a variety of insects, and are generally accompanied by a rapid rise in thoracic temperature (May, 1979). In particular, such movements are associated with thoracic heat generation in a wide variety of bumble bee species (Heinrich, 1993). Fibrillar muscles are responsible for the generation of bumble bee thoracic heat (Heinrich and Kammer, 1973), and contractions of *B. impatiens* thoracic flight muscles, particularly the dorsoventral muscle fibers, were associated with flight warm-up (Esch and Goller, 1991). In the shade (as in our experiments), the difference between ambient and thoracic temperatures is primarily a result of flight metabolism or thermoregulation through muscular activity during the times when they are perched on flowers (Heinrich, 1972a).

Previous studies hint at a similar effect of food quality on T_{th} . When Heinrich added concentrated, viscous sugar syrup to fireweed flowers, he reported that feeding *B. vagans* foragers held their wings folded dorsally with rapid abdominal respiratory movements (as we observed in our study) (Heinrich, 1972b). After 2 min of feeding, bees had an average T_{th} of 34.8°C, significantly higher ($P<0.05$) than those foraging on fireweed with normal, un-supplemented nectar at the same range of ambient air temperatures. There were significant

differences in T_{th} based upon flower type: higher T_{th} in bumble bees foraging on raspberry flowers than on fireweed or spiraea (Heinrich and Heinrich, 1983b). Based upon our results, we suggest that the quality of nectar reward may have contributed to some of these T_{th} differences in *B. terricola*. For *B. terricola* foraging in the field on *Asclepias syriaca* nectar, mean T_{th} was relatively independent from T_a (regulated approximately near 36°C, depending upon exposure to shade or sun), unlike mean T_{th} of bees foraging from *Spiraea latifolia* or *Solidago canadensis*, which were more strongly influenced by ambient air temperatures. Interestingly, individual *A. syriaca* flowers contained larger volumes of nectar than *S. latifolia* or *S. canadensis* flowers (Heinrich, 1972a). These results suggest that volume of a reward may also have an influence on T_{th} , as is found in honey bees, where higher nectar flow rates resulted in higher T_{th} (Waddington, 1990). We hypothesize that bumble bee forager T_{th} will be correlated generally and positively with nectar sugar content and flow rate.

Nieh and Sánchez hypothesized that all corbiculate bees possess the ability to adjust body temperature based upon food rewards (Nieh and Sánchez, 2005), and supporting data had been found in the honey bees and stingless bees (Nieh and Sánchez, 2005; Stabentheiner, 2001). The present results demonstrate that at least one species within the bumble bees increases its thoracic temperature with increased carbohydrate reward. Whether this effect can be observed in other groups of bees, such as some of the Halictidae, remains to be demonstrated, but we suggest that this is quite likely. The modulation of thoracic temperature in accordance with food value may be a widespread adaptation facilitating the rapid collection of good food in flying Hymenoptera.

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References

- Baird, J. M. (1986). A field study of thermoregulation in the carpenter bee *Xylocopa virginica virginica* (Hymenoptera: Anthophoridae). *Physiol. Zool.* **59**, 157-168.
- Baker, H. G. and Baker, I. (1982). Floral nectar sugar constituents in relation to pollinator type. In *Handbook of Experimental Pollination Biology* (ed. R. J. Little), pp. 117-141. New York: Van Nostrand Reinhold.
- Balderrama, N. M., de Almeida, B. L. O. and Nunez, J. A. (1992). Metabolic rate during foraging in the honeybee. *J. Comp. Physiol. B* **162**, 440-447.
- Blatt, J. and Rocas, F. (2001). Haemolymph sugar levels in foraging honeybees (*Apis mellifera carnica*): dependence on metabolic rate and in vivo measurement of maximal rates of trehalose synthesis. *J. Exp. Biol.* **204**, 2709-2716.
- Blatt, J. and Rocas, F. (2002). The control of the proventriculus in the honeybee (*Apis mellifera carnica* L.). I. A dynamic process influenced by food quality and quantity? *J. Insect Physiol.* **48**, 643-654.
- Bubnik, Z., Kadlec, P., Urban, D. and Bruhns, M. (1995). *Sugar Technologists Manual*. Berlin: Bartens.
- Bujok, B., Kleinhenz, M., Fuchs, S. and Tautz, J. (2002). Hot spots in the bee hive. *Naturwissenschaften* **89**, 299-301.
- Chittka, L., Dyer, A. G., Bock, F. and Dornhaus, A. (2003). Psychophysics: bees trade off foraging speed for accuracy. *Nature* **424**, 388.
- Cockerell, T. D. A. (1912). Descriptions and records of bees. *XLV. Ann. Mag. Nat. Hist.* **8**, 327-344.
- Coelho, J. R. (1991). The effect of thorax temperature on force production during tethered flight in honeybee (*Apis mellifera*) drones, workers, and queen. *Physiol. Zool.* **64**, 823-835.
- Corbet, S. A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A. and Smith, K. (1993). Temperature and the pollinating activity of social bees. *Ecol. Entomol.* **18**, 17-30.
- Dornhaus, A. and Cameron, S. (2003). A scientific note on food alert in *Bombus transversalis*. *Apidologie* **34**, 87-88.
- Dornhaus, A. and Chittka, L. (1999). Evolutionary origins of bee dances. *Nature* **401**, 38.
- Dornhaus, A. and Chittka, L. (2004). Information flow and foraging decisions in bumble bees (*Bombus* spp.). *Apidologie* **35**, 183-192.
- Dyer, A. G., Whitney, H. M., Arnold, S. E. J., Glover, B. J. and Chittka, L. (2006). Bees associate warmth with floral color. *Nature* **442**, 525.
- Dyer, C. D. and Seeley, T. D. (1987). Interspecific comparison of endothermy in honey bees (*Apis*): deviations from the expected size-related patterns. *J. Exp. Biol.* **127**, 1-26.
- Esch, H. (1960). Über die körpertemperaturen und den wärmehaushalt von *Apis mellifica*. *Z. Vergl. Physiol.* **43**, 305-335.
- Esch, H. (1976). Body temperature and flight performance of honey bees in a servomechanically controlled wind tunnel. *J. Comp. Physiol.* **109**, 254-277.
- Esch, H. and Goller, F. (1991). How do bees shiver? *Naturwissenschaften* **78**, 325-328.
- Farina, W. M. and Wainelboim, A. J. (2001). Changes in the thoracic temperature of honeybees while receiving nectar from foragers collecting at different reward rates. *J. Exp. Biol.* **204**, 1653-1658.
- Feuerbacher, E., Fewell, J. H., Roberts, S. P., Smith, E. F. and Harrison, J. F. (2003). Effects of load type (pollen or nectar) and load mass on hovering metabolic rate and mechanical power output in the honey bee *Apis mellifera*. *J. Exp. Biol.* **206**, 1855-1865.
- Heinrich, B. (1972a). Energetics of temperature regulation and foraging in a bumblebee, *Bombus terricola* Kirby. *J. Comp. Physiol.* **77**, 49-64.
- Heinrich, B. (1972b). Temperature regulation in the bumblebee *Bombus vagans*: a field study. *Science* **175**, 185-187.
- Heinrich, B. (1974). Thermoregulation in endothermic insects. *Science* **185**, 747-756.
- Heinrich, B. (1979). Thermoregulation of African and European honeybees during foraging, attack, and hive exits and returns. *J. Exp. Biol.* **80**, 217-229.
- Heinrich, B. (1993). *The Hot-blooded Insects: Strategies and Mechanisms of Thermoregulation*. Berlin: Springer-Verlag.
- Heinrich, B. and Heinrich, M. J. E. (1983a). Heterothermia in foraging workers and drones of the bumblebee *Bombus terricola*. *Physiol. Zool.* **56**, 563-567.
- Heinrich, B. and Heinrich, M. J. E. (1983b). Size and caste in temperature regulation by bumblebees. *Physiol. Zool.* **56**, 552-562.
- Heinrich, B. and Kammer, A. E. (1973). Activation of the fibrillar muscles in the bumblebee during warm-up, stabilization of thoracic temperature and flight. *J. Exp. Biol.* **58**, 677-688.
- Himmer, A. (1932). Die Temperaturverhältnisse bei den sozialen Hymenopteren. *Biol. Rev.* **7**, 224-253.
- Hölldobler, B. and Wilson, E. O. (1990). *The Ants*. Cambridge, MA: Belknap Press of Harvard University Press.
- Kleinhenz, M., Bujok, B., Fuchs, S. and Tautz, J. (2003). Hot bees in empty broodnest cells: heating from within. *J. Exp. Biol.* **206**, 4217-4231.
- Labougle, J. M. (1990). *Bombus* of Mexico and Central America (Hymenoptera, Apidae). *Uni. Kansas Sci. Bull.* **54**, 35-73.
- May, M. L. (1979). Insect thermoregulation. *Annu. Rev. Entomol.* **24**, 313-349.
- Moffatt, L. (2001). Metabolic rate and thermal stability during honeybee foraging at different reward rates. *J. Exp. Biol.* **204**, 759-766.
- Moffatt, L. and Nunez, J. A. (1997). Oxygen consumption in the foraging honeybee depends on the reward rate at the food source. *J. Comp. Physiol. B* **167**, 36-42.
- Nieh, J. C. and Sánchez, D. (2005). Effect of food quality, distance, and height on thoracic temperatures in a stingless bee, *Melipona panamica*. *J. Exp. Biol.* **208**, 3933-3943.
- Roubik, D. W., Yanega, D., Aluja, S. M., Buchmann, S. L. and Inouye, D.

- W. (1995). On optimal nectar foraging by some tropical bees (Hymenoptera: Apidae). *Apidologie* **26**, 197-211.
- Rzedowski, J.** (1978). *Vegetacion de Mexico*. Mexico: Limusa.
- Schmaranzer, S. and Stabentheiner, A.** (1988). Variability of the thermal behavior of honeybees on a feeding place. *J. Comp. Physiol. B* **158**, 135-142.
- Spaethe, J., Tautz, J. and Chittka, L.** (2001). Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. *Proc. Natl. Acad. Sci. USA* **98**, 3898-3903.
- Stabentheiner, A.** (1996). Effect of foraging distance on the thermal behaviour of honeybees during dancing, walking and trophallaxis. *Ethology* **102**, 360-370.
- Stabentheiner, A.** (2001). Thermoregulation of dancing bees: thoracic temperature of pollen and nectar foragers in relation to profitability of foraging and colony need. *J. Insect Physiol.* **47**, 385-392.
- Stabentheiner, A. and Hagmüller, K.** (1991). Sweet food means hot dancing in honeybees. *Naturwissenschaften* **78**, 471-473.
- Stabentheiner, A. and Schmaranzer, S.** (1987). Thermographic determination of body temperatures in honey bees and hornets: calibration and applications. *Thermology* **2**, 563-572.
- Stabentheiner, A., Hagmüller, K. and Kovac, H.** (1990). Thermisches Verhalten von Hongibienen im Schwänzeltanz. *Verh. Dtsch. Zool. Ges.* **83**, 624.
- Stabentheiner, A., Kovac, H. and Hagmüller, K.** (1995). Thermal behavior of round and wagtail dancing honeybees. *J. Comp. Physiol. B* **165**, 433-444.
- Stabentheiner, A., Helmut, K. and Schmaranzer, S.** (2004). Der Einfluss der Eonnenstrahlung auf die Körpertemperatur Wasser sammelnder Wespen (*Paravespula germanica*). *Mitt. Dtsch. Ges. Allg. Angew. Entomol.* **14**, 451-454.
- Stone, G. N.** (1993). Thermoregulation in four species of tropical solitary bees: the roles of size, sex and altitude. *J. Comp. Physiol. B* **163**, 317-326.
- Stone, G. N.** (1994). Patterns of evolution of warm-up rates and body temperatures in flight in solitary bees of the genus *Anthophora*. *Funct. Ecol.* **8**, 324-335.
- Stone, G. N. and Willmer, P. G.** (1989). Warm-up rates and body temperatures in bees: the importance of body size, thermal regime, and phylogeny. *J. Exp. Biol.* **147**, 303-328.
- Underwood, B. A.** (1991). Thermoregulation and energetic decision-making by the honeybees *Apis cerana*, *Apis dorsata* and *Apis laboriosa*. *J. Exp. Biol.* **157**, 19-34.
- von Frisch, K.** (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA: Belknap Press.
- Waddington, K. D.** (1990). Foraging profits and thoracic temperature of honey bees (*Apis mellifera*). *J. Comp. Physiol. B* **160**, 325-329.
- Zar, J. H.** (1984). *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall.