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Honeybee waggle dances: the "energy hypothesis" and thermoregulatory behavior of foragers

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Abstract. Honeybees were trained to visit artificial feeding sites containing a 2 mol · l^{-1} sucrose solution. To reach the feeder they either had to walk through 3 m of Teflon tube, or fly 20 m or 65 m and then walk through 3 m of tube. Only individuals that flew at least 65 m performed waggle dances. The distance indicated in these waggle dances, judged by the number of wagging movements per wagrun, was the same regardless of whether individuals had to run an additional 3 m of tube after flight or not. The energy needed during walking after flight was determined by measuring O_2 consumption. All individuals attempted to regulate their body temperatures between 36 and 42° C during walking and feeding (O_2 consumption = 40 μl · min^{-1} per bee). Calculations show that this walking through 3 m of tube requires as much energy as flying 128 m (difference between thoracic and ambient temperature = 15° C). This energy expenditure was not reflected in the dances. The results do not support the hypothesis that honeybees estimate feeding site distances by measuring the energy required to reach a feeder.

Key words: Energy – Dances – Temperature – Oxygen – Honeybees, *Apis mellifera*

Introduction

Waggle dances of honeybees contain distinct correlates of distance to the feeding site. Karl von Frisch (1967) proposed that foragers estimate the distance to the feeding site through energy expenditure on their flight to this food source (the "energy hypothesis"). Support for this hypothesis was provided by a number of experiments where, through manipulations, energy expenditure was increased. Honeybees affected in this manner indicated greater distances in their subsequent dances than control foragers.

Heran's (1956) mountain experiments provided the strongest support for the energy hypothesis: bees that flew up a steep mountain slope to reach the feeding site indicated generally greater distances in their dances than bees foraging at equidistant feeders down the mountain slope. Thus, the greater energy requirements of the uphill group were reflected in their distance indication. However, a recent attempt to duplicate these results under more controlled conditions did not support the predictions of the energy hypothesis (Goller and Esch 1990).

Other manipulations to increase energy requirements for foragers on their flight involved addition of weight and increased air resistance (Schifferer 1952; von Frisch 1967). Results from these experiments also supported the energy hypothesis. However, recent attempts to replicate these experiments did not agree with the predictions of the energy hypothesis (Neese 1988; F. Goller and H. Esch, unpublished data).

Strong support for the energy hypothesis was also derived from experiments where foragers walked part of the distance to the feeding site (Bisetzky 1957). Bees which had walked 3 m indicated feeder distances of 50–100 m in their dances. Scholze et al. (1964) determined energy consumption rates for flying and walking bees indirectly and concluded that energy requirements for flight and walking matched the respective distance indications, as found by Bisetzky (1957).

There are some obvious problems with this indirectly derived support. Energy requirements were determined from sugar consumption rates in bees that did not actually forage. In walking bees, energy expenditure resulting from leg muscle activity alone could not account for the estimated expenditure (Scholze et al. 1964). It can be assumed that these bees were attempting to regulate their T_{th} and most of the energy would have been actually consumed by the flight muscles (Goller and Esch 1991). It

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Abbreviations: T_a ambient temperature; T_b, body temperature; T_{th} thorax temperature

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is not possible to interpret their findings in the context of Bisetzky's (1957) data since T_as were not reported. Moreover, bees used in the study by Scholze et al. (1964) did not walk towards an actual feeding site but walked towards a light source which may greatly affect their motivation and thus energy expenditure for thermoregulation. In addition, energy requirements for flight were determined for bees flying on a tether which is known to underestimate power requirements for free flight (Rothe and Nachtigall 1989).

In this study we therefore reinvestigated dance behavior of honey bees after they had covered part of the distance to a food source by walking, and measured energy expenditure directly as O_2 consumption rates while bees were walking to the food source and during imbibition. The results show clearly that honeybees do not indicate greater distances after walking to a food source. They also show that energy requirements during walking depend on T_a and are not necessarily comparable to those during flight. Thus, this study casts doubt on this line of supportive evidence for the energy hypothesis.

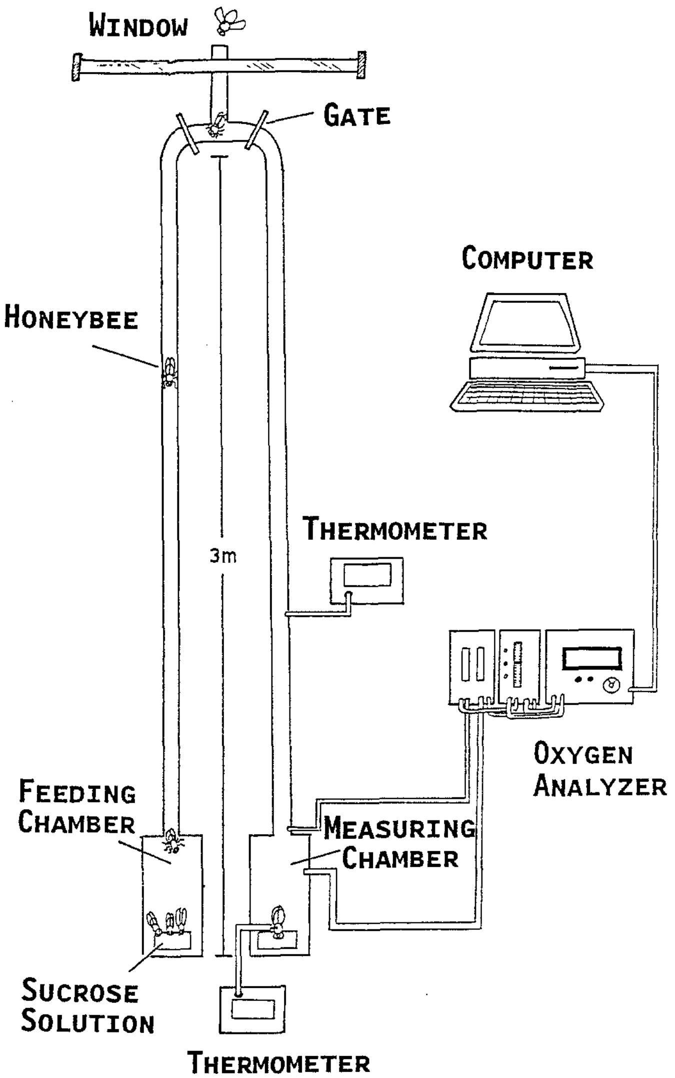

Fig. 1. The experimental setup. The tube system is seen from above. After entering the tube outside the laboratory window individuals can either be gated to the feeding or the measuring chamber

Materials and methods

Honeybees (*Apis mellifera ligustica*) from stocks in the Department of Biological Sciences at the University of Notre Dame were kept in two or three frame observation hives (von Frisch 1967). Individuals were either trained to a feeder at the end of a clear 3-m Teflon tube (inner diameter 2.7 cm) directly connected to the hive, or they were trained to feeders in front of a Teflon tube reached after 20 or 65 m of flight. A 2 mol · l^{-1} sucrose solution in a pneumatic feeding bowl was used in all experiments. Dances were videotaped immediately after return from the feeder. Individuals at the 20 and 65 m feeders were enticed to enter the tube, and to walk to the feeder at its end. The length of the tube was gradually extended to 3 m during training. Dances of bees who had flown 20 or 65 m and then had walked through 3 m of tube were videotaped upon return to the hive. All tapes were evaluated during replay in slow motion. The number of waggles per wagrun and timing of other dance movements were determined with a DTK Peer-2030 computer, a Redlake Spectrum NTSC frame grabber, and the OPTIMAS program system.

O_2 consumption of individual bees was measured with an Ametek Oxygen Analyzer (Model S-3A, Ametek/Thermox Instruments, Pittsburg, USA) in open-flow mode (flow rate 100 ml · min^{-1}). O_2 content of air taken from the feeder bottle was compared with samples taken from the access tube (distance between sampling points 10 cm). A computer determined the analyzer output six times per s and recorded 1.6-s averages on disk. Calibration with N_2 confirmed the plateau readings. T_a was measured by a thermocouple in the tube. The T_b of foragers was determined with a second thermocouple: it was repeatedly inserted into a small drop of heat-sink grease (Radio Shack 276–1372) in the middle of the forager's notum through a small hole in the tube wall. The heat-sink grease remained on the thorax for several days, allowing repeated observations on the same individuals.

The Teflon tube at the 65-m site was inside a laboratory with its entrance opening through a window. Tube temperature could be controlled by the laboratory's T_a. A switch near the tube entrance allowed "shunting" of unwanted visitors into a second, parallel tube. Only one individual at a time was allowed in the measuring chamber (Fig. 1).

Results

Most individuals tried to maintain T_{th} between 36 and 42°C, independent of the T_a, while running through the tube (Fig. 2). O_2 consumption reflected the difference between thoracic and ambient temperature; it was almost 40 µl · min^{-1} per bee at a temperature difference of 15° C (Fig. 3). O_2 consumption and T_{th} remained elevated during the uptake of food (Fig. 4).

Only foragers visiting the 65-m feeding site performed waggle dances. Communicated feeder distances were determined by counting the number of waggles per wagrun. The results under various experimental conditions are shown in Table 1. Foragers which had flown 65 m and visited the feeder *at the entrance of the tube* indicated a distance not significantly different from that given by foragers which had flown 65 m and then walked an additional 3 m to the feeder *at the end of the tube.*

The "distance curve" (based on waggles per wagrun) for the bees used is shown in Fig. 5. The slope of this curve is very steep near 65 m, where waggle per wagrun measurements and related O_2 determinations were made. Even small increases in distance estimation by foragers should have led to noticeable changes in dancing behavior.

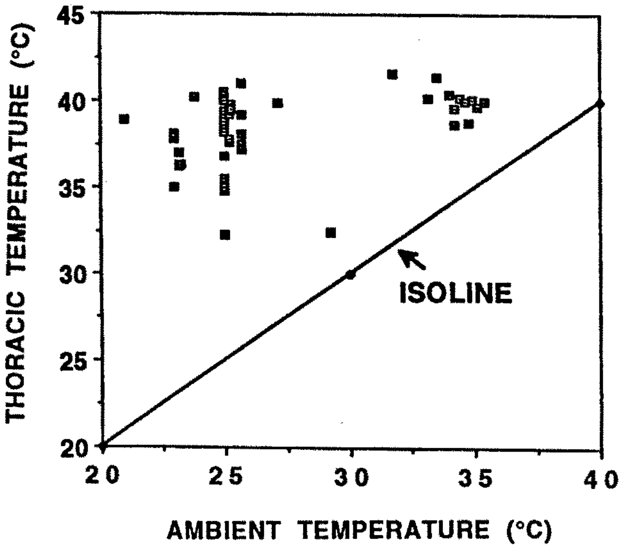

Fig. 2. Thoracic temperatures of foragers in the measuring chamber at various ambient temperatures (based on eight individuals)

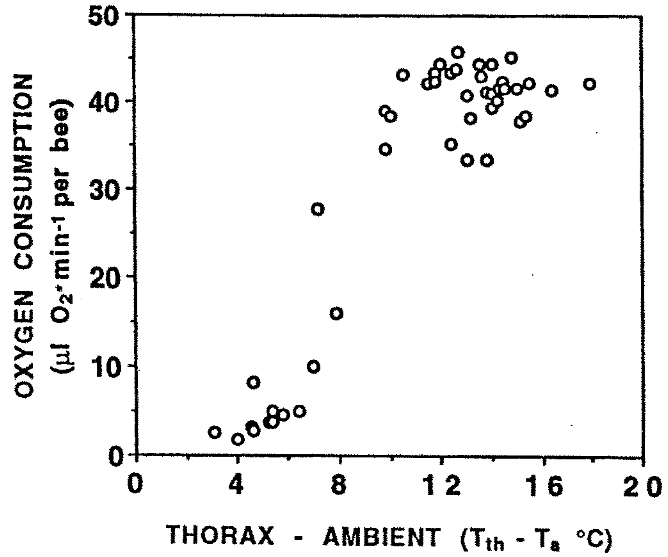

Fig. 3. Oxygen consumption and temperature difference between thorax and environment in the measuring chamber (based on eight individuals)

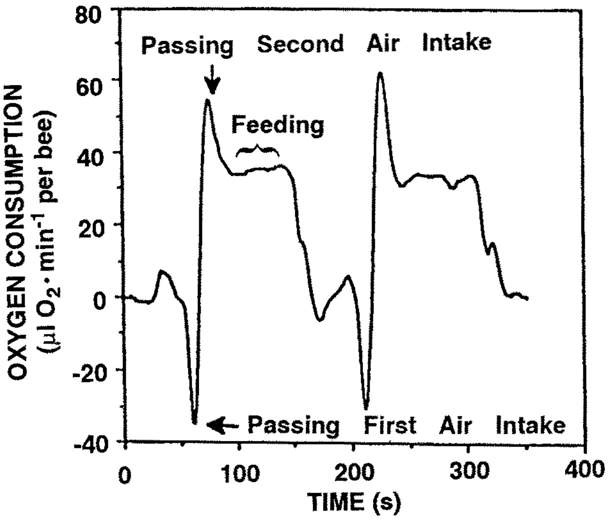

Fig. 4. Oxygen consumption at the tube feeder, showing two imbibition episodes. The oxygen analyzer compares O_2 content of air drawn from a "measuring" and a "reference" air intake. The figure shows increasing O_2 consumption when O_2 content of "measuring" air is *lower* than O_2 content of "reference" air. A negative peak appears when a bee approaches the feeder and passes the reference (*first*) air intake ("measuring" air contains *more* O_2 than "reference" air). The positive peak occurs when the bee then passes the measuring intake (*second*) ("measuring" air contains *less* O_2 than "reference" air). The plateau indicates actual O_2 consumption in the feeding chamber. The feeding chamber was calibrated with O_2 depleted air. T_a = 25° C

Foragers which visited the feeder at the end of 3 m of tube after flying 20 m performed round dances, interspersed with waggle movements. There were no obvious differences between these round dances and dances for a feeding site at the entrance to the tube. Foragers which walked through 3 m of tube directly from the hive also performed round dances with interspersed waggle movements.

Discussion

Several investigators have concluded that bees can not separate energy consumed in flight from energy consumed during walking when estimating the feeder dis-

Table 1. Comparison of observed and predicted distance indication by waggles

	Average number of waggles ± 1 SE	*n*
Observed values		
Feeder at tube entrance (65 m)	2.98 ± 0.03	1173
Feeder at end of tube (65 m + 3 m)	3.49 ± 0.03	1279
Predicted values		
Value for foragers which walked 3 m and flew 65 m:		
Scholze et al. (1964)	5.50	
O_2 measurements in this study	7.40	

Observations at T_a = 25 °C

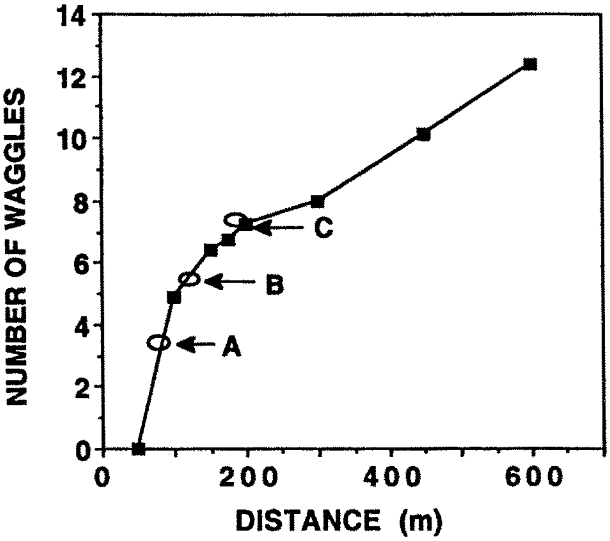

Fig. 5. The relationship between feeder distance and number of waggles per wagrun (■) for the hive used in our experiments (based on 11 foragers). Bees that flew 65 m and walked through 3 m of tube actually indicated 68 m (**A**). Using the energy consumed, as determined by Scholze et al. (1964) they should have indicated 120 m (**B**) (65 m flight + 3 m walking, 3 m walking ≙ 55 m flight). Using the O_2 consumption determined in this study foragers should indicate 193 m (**C**) (65 m of flight + O_2 for 128 m of flight)

tance (Bisetzky 1957; Scholze et al. 1964; von Frisch 1967; Gonçalves 1969).

Our measurements of energy expenditure show clearly that bees walking to the food source attempted to regulate their T_{th} to about 40 °C. The absolute metabolic rate during walking depends on the T_a. These observations are not unexpected. Thermographic measurements revealed that foragers arrive at feeders 335 m from the hive with T_bs near 40 °C (0.5 mol · l^{-1} sucrose solution) and try to maintain this temperature during feeding (Schmaranzer and Stabentheiner 1988). The behavior of foragers at our 65-m tube feeding site is very similar in many respects: foragers arriving at the tube entrance with high T_bs maintain this temperature while running to the feeder, during feeding, and until they depart.

Our measurements allow an exact determination of the energy needed to reach the feeding site by walking, allowing prediction of the additional distance dancers should have indicated if they had used all the expended energy for distance estimation. Foragers took an average of 40 s to walk from tube entrance to feeder. O_2 consumption of an individual during this time span was 27 μl O_2 (at 40 μl · min^{-1} per bee, $T_{th}-T_a = 15$ °C, Fig. 3). Dance observations shown in Table 1 were made at this temperature difference. This O_2 consumption would sustain 16 s of flight at a metabolic rate of 100 μl · min^{-1} per bee (Bastian and Esch 1970; Rothe and Nachtigall 1989). At a flight velocity of 8 m · s^{-1} (von Frisch 1967) an individual could fly 128 m during this time. Dancers should thus have made approximately 7,4 waggles per wagrun, as read from the distance curve in Fig. 5 (65 m + 128 m = 193 m), if they had included the additional energy expenditure in their distance estimation. *Foragers did not show such an increase in waggles per wagrun after walking*. In this context it is interesting to note that distance estimation by *Cataglyphis* ants is not affected by loads of up to four times their body weight (R. Wehner, Zürich, personal communication).

Scholze et al. (1964) estimated the energy consumption for walking a distance of 3 m as being equivalent to flying 55 m. Using this estimate foragers that flew 65 m and then walked for 3 m should have indicated 120 m (65 m + 55 m). However, the estimate that walking for 3 m is equivalent to 55 m flight is probably too low. Walking bees in the study by Scholze et al. (1954) did not actually go to a food source and probably did not warm up as much as foragers, and flying bees flew hanging from a carousel. Even if their estimate was correct, it still would not correctly predict the distance indication given by walking bees in the present study (Table 1).

T_b is raised by shivering with flight muscles (Esch et al. 1991). Almost all of the O_2 consumption that can be determined with the methods used in the present study is expended by shivering. Much less O_2 is consumed by leg muscle contractions during walking and by "resting metabolism" [<1 μl · min^{-1} per bee; Goller and Esch (1991)].

The observations of Bisetzky (1957) that bees perform waggle dances after walking 3 m are puzzling. Only Gonçalves (1969) seems to have been able to confirm these observations, even though he states that "the returning marked bee danced in the hive, performing a figure-of-eight dance which gave the correct direction but with more variation than Bisetzky (1957) observed". We did not see figure-of-eight dances under these circumstances, even though we used the same bee species (*Apis mellifera ligustica*) as Gonçalves (1969). Other researchers who tried to confirm Bisetzky's (1957) observations (Gould 1975; K. Waddington, personal communication) had great difficulty finding regularly repeated waggle dances. It is possible that the wagging episodes in round dances were mistaken for wagging runs. Bees who visited a feeder after walking at least 3 m, even after flying 20 m before entering the tube, clearly performed only round dances with interspersed wagging runs that pointed in various directions.

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