WHY HONEY BEES HAVE DIFFERENT DANCE RHYTHMS

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ABSTRACT: Bees determine distance by how much energy they spend during the outgoing flight (Heran 1955). It is proposed that energy expenditure is measured by a bee as a proportion of her total available energy. Dancing speed and size can be correlated. Dance rhythm seems to be genetically determined (Boch 1957, Lindauer 1971, Gould 1982) because it is measured within the human conceptual time-space frame. The bee's dances, however, are based on energetics and energetics is influenced by variables such as size which are not considered when dance rhythms are compared.

In evolutionary time energetics has influenced size. In colder climates larger bodies, with energetics better suited for heat conservation, have been selected (Rensch 1983). This explains the latitudinal pattern of dance rhythms (Gould 1982) and gives reason to believe that organisms as integrated wholes (Riedl 1983) evolve in interaction with the environment.

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INTRODUCTION

The honey bee's dances convey direction and distance, the two quantitative parameters necessary to find a certain location. Direction as angle to the sun is represented inside the dark hive with the same angular relationship to gravity. Distance is indicated by the number of waggles which are performed during the straight run of the figure-eight dances. The farther away the reported food source, the greater is the number of waggles per run. Consequently it takes the bee longer to complete the whole dance cycle and the rhythm of the dance becomes slower. Variations in the dance rhythm when different bees indicate the same distance are called dialects (Frisch 1966). Gould (1982) concluded that the geographic distribution of what he called long- and short-distance dialects is the outcome of natural selection. Bees living farther north have to forage in a larger area to support their colonies through the colder winters. Therefore the long-distance dialect with fewer waggles in the straight run is selected in the Austrian bee, A.m. carnica. The short-distance dialect, with more waggles for the same distance, is employed by the more southern Italian bee, A.m. ligustica. Data for the Egyptian bee, A.m. fasciata, from Boch (1957) fit into this picture. Gould concluded that "each case represents a compromise in the face of competing selection pressures". The compromise is between the efficiency of the long-distance dialect and the precision of the short-distance dialect.

Direction and distance communication in general.
In order to communicate the value of a variable parameter it is necessary that measurements are made in relation to a reasonably fixed point to which all communicating parties can refer. To determine and indicate direction bees normally relate to the sun and gravity. In human societies the commonly used reference points east, west, north and south are also sun-related. Our unit for measuring distance was originally defined in reference to the earth as the ten-millionth part of the meridian quadrant. In earlier times distance was often measured in reference to the work done by the human body. To cite but one example: "mile" is derived from the Latin "milia passuum" which means 1000 steps. Observations show that bees measure distance by how much energy they spend during the outgoing flight (Heran 1955). As measuring device and as a reference bees can use only their bodies. Therefore I propose that a bee measures the distance by registering what proportion of her total available energy she spends. Encoded as dance rhythm and understood

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by other bees is the amount of energy spent in relation to their capacity for energy
production.

Dance rhythm is based on energy expenditure and depends on metabolism.

When the flight from the hive to the food takes place against a head wind or uphill (Heran
1955) or at low temperatures (Heran 1955, Werner 1954) a bee has to use more energy.
Consequently she includes more waggles in her straight run, which makes her dance rhythm
slower. This indicates to the observer a longer distance than she has actually flown.
Werner (1954) found that dancing speed was increased by administering andrenalin and
thyroxin, and it was slowed by strichnine. Probably this happened because these substances
influence in the same way general activity, as measured by timing a phototactic wingless
run, and metabolism, as measured by oxygen consumption. Schricker (1974, reported in Gould
1976) could show that dancers under the influence of parathion shortened the duration of the
waggle dances. Consequently recruited foragers looked for food at a shorter distance.

Racial differences in dance rhythms are seen when the dancing speeds of different bees
announcing the same distance are compared. It has been assumed that these differences show
degrees of the genetic relationship (Boch 1957, Lindauer 1971, Gould 1982). Boch (1957)
plotted dancing speed of different honey bees against the logarithm of distance and found
that the regression lines run almost parallel. Furthermore "In approximately the same
sequence each race (when the feeding place is taken step-wise farther from the hive)
switches from the round dance to the direction-indicating waggle dance, so they pass after
each other the threshold of a certain dancing speed" (Boch 1957:316). These results suggest
that the mechanism underlying the dance rhythm might be the same for all honey bees and that
one varying factor could determine the differences.

Size is a characteristic which varies widely among honey-bee races. When the different
races of Apis mellifera are ranked according to size other characteristics fall into the
same pattern.

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Dancing characteristics of Apis mellifera races related to size

Race of A. mel-lifera	Length of front wing mm	Drinking capacity mm^3	Beginning of waggle m from hive	No. of waggle runs in 15 sec. distance of 200m	400m
carnica	9.6-9.3	56.7	85	8.45	6.75
mellifera	9.5		65	7.85	6.0
intermissa	9.25	54.5	65	7.8	5.9
caucasica	9.32		35	7.3	5.6
ligusta	9.2		35	7.3	5.85
fasciata	7.8	37.2	12	6.1	4.6

(Compiled From Data in Boch (1957)

It should be noted that wing length is not a very good indicator of size because bigger bees
in colder climates have relative shorter wings (Alpatov 1927). Thus size difference might
be greater than indicated by wing length, a measurement easily obtained.

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The same correlation between size and dancing rhythm is found when the species of
tropical honey bees are compared:

	Length of fore wing in mm	Number of runs per 15 sec. distance of 200m	400m
A. dorsata	13.0	7.4	6.6
A. cerana	8.5	5.5	3.8
A. florea	5.2	4.5	-

According to Lindauer 1971.

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If, as proposed, the bee encodes the relative amount of energy spent, size must influence dance rhythm. When both a small bee and a big bee fly the same distance, the bigger bee spends a smaller proportion of her available energy and consequently dances faster. Thus dance rhythm depends on the bee's total energy economy.
An integration according to size of all honey-bee species and A. mellifera races will not yield a straight correlation between size and rhythm. Probably because environmental factors play an overriding role when bees of the tropics are compared with those foraging in a temperate climate. Even if the temperature is higher in the tropics, flying in the more humid and therefore denser air might be more energy-consuming. Foraging in the shade of the forest compared to the open sunny meadows could also make a difference. Internal factors could influence efficiency. Tropical honey bees are in some ways more primitive than A. mellifera (Lindauer 1971).

A metaphor can explain how bees might communicate distance. Assuming that all cars are built with the capacity of their fuel tanks proportional to their size. They run with the same efficiency under equal road conditions. Drivers of cars of the same size can tell each other how far to go by monitering the relative amount of fuel in their tanks. (e.g. go till tank is half empty). Speed does not matter. If, however, information on this basis is exchanged by drivers of different-sized cars, distance will be miscalculated by the receiver of the message. The same misunderstandings occur when different bees are put together to make a mixed colony (Boch 1947).

> "If, for example an Austrian bee receives information
> from an Italian bee about a food place 100 meters from
> the nest, she will fly 120 meters, because she interprets
> the 'Italian dialect' in her Austrian way. And con-
> versely the Italian bee will fly only 80 meters when given
> information for 100 meters by an Austrain bee" (Lindauer 1971:61)

The Italian bee (A.m. ligustica) is a little smaller than the Austrian bee (A.m. carnica) and has a more slender body.

In earlier experiments (Steche 1954, reported in Boch 1957) a greater number of bees misunderstood the information. Such different results could be expected if dance rhythm is not a racial characteristic but depends on the energetics of the bees.

To calculate the energetics of a bee many factors have to be considered. Heinrich (1972) measured specific heat, time, glucose consumption, temerpature and weight. The metabolic rate of flying insects is a function of body mass and body-air temperature gradient (Peters 1983:67). The calculation of metabolic rates makes it possible to compare the energy consumption of different animals. Metabolic rate can be described as a linear function of body mass raised to an exponent of approximately 3/4. This seems to hold true for all animals (Peters 1983:45). If, however, a bee measures her flight in terms of how much of her energy she spends, her metabolic rate is of no consequence. She registers only the relative amount of energy and not how fast it is spent. Flight duration does not influence dance rhythm (Heran 1955). Specific heat is the same for all bees. Thus dance rhythm should depend on weight, provided that those environmental factors which also influence the energetics of a bee are very similar.
How can bees measure energy expenditure? In mixed-hive studies Witherell and Laidlow (1971) compared morphological and behavioral aspects of a mutant with diminutive wings with normal bees (Italian).

> "However, contrary to expectations that di-bees would execute dances indicating
> "longer" distances than would normal bees,there was only a slight, nonsignificant
> difference between the two groups with respect to either the duration of waggle-runs
> or the dance tempo, after returning from the same distance. Perhaps this can be best
> explained on the following basis. Since the wing area of di-bees averages only 62.9
> percent of normal, the wings encounter less air resistance in flight, and thus beat
> 22.2 percent faster than do normal wings.......Hence, di-bees probably expend little,
> if any, more energy in flight than do normal bees, and so do not indicate a "greater
> distance" in their dance maneuvers" (Witherell and Laidlow 1977).

Weight of the bees has not been considered by the authors in this connection but might account for the only "slight, statistically nonsignificant" difference in dancing speed. The weight after the removal of the honey stomach of di-bees was outflying 94.7% and returning 98.1% of the weight of normal bees. At 250 m the number of waggles runs per 15 seconds was 7.1 for di and 7.9 for normal; at 1000 m, it was 3.8 for di and 4.0 for normal. The sample number was rather small.

When the wing area is experimentally decreased, the bees compensate by increasing the stroke frequency accordingly (Satavalta 1947, Wenner 1954). Stroke frequencies do not depend directly on the action potentials measured in the indirect flight muscle, which suggests that the wing-beat rate is adjusted by a sensory-feedback mechanism (Bastian and Esch 1970). This seems to indicate that energy consumption per flown distance remains nearly the same for short- and long-winged bees, and wing-beat frequency cannot play any role in distance measuring.

One cannot assume that bees are able to register O_2 consumption or CO_2 production, which are often measured in experiments to determine energy expenditure. The decrease of glucose in their bodies could be detected by bees. Mature, adult bees seem to feed exclusively on nectar (Dietz 1975). Normally, bees do not stop to feed during their flight to the target. Organisms, in general, can monitor the relative amount of substances in their blood. Thus, it is not unreasonable to assume that such a mechanism is employed as part of the dance communication. Perhaps a proportion of the glucose needed for the scouting flight is used to perform the waggle dance, which is "a miniaturized version of the flight from the hive to the target" (Wilson 1975:177). But even if the waggle run is "nothing but a reenaction of the flight, the bee will take to the target" (Wilson 1977:177), we still do not know how the other bees understand it. But regardless of what is monitored and how it is encoded and understood, measurement of energy expenditure and its expression in the dances is relative to the capacity for energy production. Therefore, it is possible for the human observer to correlate dancing rhythm with size, when all other parameters which influence the bee's energetics are nearly the same.

Biological significance of distance communication. Only bees with "complex behavioral and physiological mechanisms for controlling and stabilizing the environment and hereby minimizing size variations" (Waddington 1980) could have evolved a complex communication system. Waddington, however, considered only misunderstandings which would arise among bees with short and long tongues over the profitability of flowers with long corollas. Another factor minimizes size variation in a bee hive. Division of labor is not achieved by different castes but by temporal assignments in the life of each worker bee. Energetics-based distance communication requires that, at any given time, all communicating bees, and that excludes the bigger drones, are approximately the same size. Even if some recruits fail to find the indicated area or take a long time to arrive there, a colony which can direct a work force to a target area has increased survival chances. It is not necessary to pinpoint a place. Flowers grow in patches and once on location bees find them by sight and smell (Frisch 1966). Thus, distance indication based on the energetics of individual bees is precise enough to allow a colony to take advantage quickly of a food source that might be available for a limited time only. Recruits which go astray, even unexperienced ones, could find a new food source. There seems to be no strong selection pressure for a "perfect system".

The different worlds of bee and man. Bees might measure their way in terms of how much of their energy is spent, by monitoring the relative amount of glucose in their bodies. We do not know how it is encoded and understood. The only code we understand is: same number of waggles - same proportion of the sender's and the receivers' energy. Measuring the expansion of space as distance is not involved.

Piaget (1979, 1972) has found that our spacial and temporal conceptions are constructed during early childhood by ordering experiences and abstracting from them the conceptual frame that we call space and time. In Einstein's universe and in the bee's world there conceptions do not exist. Only the human mind builds up a conceptual framework in which space expands equally far into all directions and, therefore, can be measured

absolutely. Our three-dimensional space is distinct from time which for us extends equally fast into past and future and, therefore, can also be measured absolutely. Thus we are able to time the bee's dances and measure the distance of their flight. Then standing on "our" baseline of "same distance" we compare the dance rhythms. It is only our absolute measuring system which tempts us to see the dance rhythm as something fixed which could be determined by competing genes (Gould 1982).

The energetics-based distance indication of the bees appears predetermined when projected into our time-space frame, because parameters such as size which influence the bees' energetics and consequently their dances, are neglected.

Geographic pattern of dance rhythms. Apis mellifera, the European honey bee, has several ecological races with transition forms at the boundaries. Gould (1982) correlated dancing speed to latitude. The common names of A.m. carnica, A.m. ligusta and A.m. fasciata, which are Austrian, Italian and Egyptian bees respectively, reflect their geographic distribution. The Austrian bee, which is the biggest bee, lives farthest north and has the fastest dance rhythm. The Egyptian bee, whose habitat is farthest south, is 10% smaller, measured linearly, than the Austrian bee and has the slowest dance rhythm. The Italian bee is in the middle regarding size, dancing speed, and latitude of habitat. Bees in Russia increase in size from south to north (Alpatov 1929). The races of the Indian honey bee, Apis cerana, in Afghanistan, Himalaya and China are larger than those of the south in Ceylon and Indonesia (Ruttner 1975). Also, bees are larger whose habitats are at higher altitudes, such as A.m intermissa in the North African Atlas range and A.m. caucasica.

Georgrapic races of many bird and mammal species show differences in average body size. The colder the climate of their habitat due to higher latitude or altitude, the larger are their bodies with relative shorter appendages (Rensch 1983). Explanation for these observations is found in the energy economy of stockier bodies that have a volume-surface ratio more favorable to heat conservation, which is important in colder climates. It seems that honey bees follow rules observed in homeothermic animals. Honey bees, just as warm-blooded animals, survive the winter by generating their own heat, keeping the nest temperature well above freezing regardless of outside temperature (Lindauer 1971, Seeley 1982). Stockier bodies are also better for bees which sit on the outside of the cluster acting as an insulation shield (Seeley 1983). Even a slight increase in heat-conservation ability will allow bees to forage on colder days, making it possible to collect more food. Thus the survival chance of a whole colony is increased in several ways and the selection pressure in colder climates is for bigger bees. Since dance rhythm is influenced by size the latitudinal pattern found by Gould (1982) is explained.

Conclusion. Dance rhythm can be correlated to size when bees measure energy expenditure as a proportion of their total available energy. When both a big and a small bee fly the same distance, the big bee spends a smaller proportion of her energy and consequently dances faster. In colder climates the selection pressure is for larger bodies whose energetics are better suited for heat conservation (Rensch 1983). Bigger bees fly farther and dance faster. There is no need to assume that competing genes code for a certain dance rhythm and are selected independently (Gould 82). Organisms might evolve as integrated wholes in interaction with the environment.

If, as proposed, it is possible to reduce at least one aspect of the bee's dances (distance measuring) to physiology, one could believe that distance information is really contained in the dance maneuvers without "attributing to the honey bees either a human psychic level or a whole host of "genetically predermined instincts" (Rosin 1984:440).

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