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A comparison of the dance language in *Apis mellifera carnica* and *Apis florea* reveals striking similarities

**Authors: Sarma · Esch · Tautz**

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Original Paper

# A comparison of the dance language in *Apis mellifera carnica* and *Apis florea* reveals striking similarities

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**Abstract** Honeybees have a dance language by which successful foragers inform nestmates about attractive food patches. The classical concept of dialects in the dance language of honeybees points to two differences in the dances by different species and races, firstly in the flight distance at which the dancers start performing waggle dances instead of round dances, and secondly in the circuit duration of the waggle dance performed for a given flight distance. However, recent findings have indicated that the dance language is influenced and affected by a number of parameters, both genetic and environmental. The current study was carried out to see whether the distance at which dancers change from round dances to waggle dances is statistically different in two different species, *Apis mellifera carnica* and *A. florea* and to develop a set of definitions for such comparative studies. Results show that the two species do not differ in the relative proportion of waggle dances and round dances performed at a given distance. Thus, this study points to the need of addressing the dialect question again.

## Introduction

Karl von Frisch reported that when successful foragers discover a profitable food patch within a radius of 20 m from the hive, the dancers execute round dances in which there is no distance information given (Frisch 1967). However, later studies showed that distance information is often given during short waggle phases which have no particular direction orientation up to a distance of 15 m (Kirchner et al. 1988; Jensen et al. 1997). When the food source is at a distance of 80 m, dancers execute true waggle dances in which the direction of the waggle phase indicates the direction to the food source. At intermediate distances, the number of waggle dances increase steadily (Boch 1957). By his criteria, he also found that the distance at which dancers started performing waggle dances differed from race to race, e.g. *Apis mellifera carnica* by his criteria made “true” waggle dances only at 80 m. However, his data indicate that dancers also waggle with some frequency at shorter distances (e.g. 20 m).

Martin Lindauer (1956) carried out observations on Asian species (*A. cerana*, *A. florea*, *A. dorsata*) and reported that there were differences in the distance at which dancers changed from round dances to waggle dances. The transition distance was much closer for the Asian species, e.g. he reported that *A. florea* started wagging when the feeder was only 5 m from the hive. Lindauer (1956) and Boch (1957) also reported inter-specific/inter-racial differences in the dance tempo (dance circuits per 15 s) at a given distance. Thus, for the same distance, different races or species would execute a different number of circuits per unit time.

According to the published dialect curves (Lindauer 1956; Boch 1957), *A. florea*, the Asian dwarf honeybee and *A. m. carnica*, the honeybee common in Germany and Austria, display the most striking differences in their dialects and the transition distance where dancers start making predominantly waggle dances. In *A. florea* this distance is 5 m from the hive, while in *A. m. carnica*, it is 80 m.

Thus, the concept of dialects in the honeybee dance language was established which basically pointed to two differences in the dances by different species and races, firstly in the flight distance at which the dancers start performing waggle dances instead of round dances, and secondly in the circuit duration of the waggle dance performed by dancers for a given flight distance.

Two recent findings motivated us to take up the question of differences in the dance language again. First, the waggle phase (not the entire circuit) is the most reliable indicator of distance and

direction of the food source (Michelsen et al. 1992; Tautz et al 1996; Seeley et al. 2000), which could not be looked at separately in the earlier studies. Second, recent studies indicate that the tendency to perform a given dance type (round versus waggle) might be inherited as a single locus trait with multiple alleles, which are inherited in a simple Mendelian fashion (Oldroyd et al. 1991; Rinderer and Beaman 1995; Johnson et al. 2002), while the visually based perception of distance is influenced by the landscape in the flight route of the forager bee, thus affecting distance indication in the dance (Srinivasan et al. 2000; Esch et al. 2001). Therefore, a number of factors could influence the tendency of a dancer to perform round or waggle dances for a feeder distance potentially giving rise to variations.

## **Materials and methods**

### **Species**

Two colonies of *A. florea* were used for the study in Bangalore, India, which were transplanted from their natural nesting sites into suitable locations in the Indian Institute of Science campus. Two colonies of *A. m. carnica* were used, one obtained from the bee station of University of Wuerzburg, Germany and transferred to Gieshügel, Wuerzburg and the second obtained from the Bee Research Institute at Lunz Am See, Austria and then transferred to a spot near the village of Lunz Am See. The *A. m. carnica* colonies were housed in observation hives and had brood and honey and pollen stores. Since *A. florea* is an open-nesting species and its dance floor is situated on the exposed horizontal part of the colony, there was no need to manipulate the colonies in any manner. The colonies used occur naturally in the locality around Bangalore and although the species is not domesticated, it is a traditional source of honey for indigenous people. *A. florea* is reproductively isolated from other species of honeybees. The *A. m. carnica* that we used in Würzburg, Germany were obtained from the local breeding centre, which uses traditional methods to ensure that racial admixture does not occur. The colony used at Lunz Am See came from a stock that is being extensively bred in the Institute and guaranteed to have been isolated from other races of *A. mellifera*.

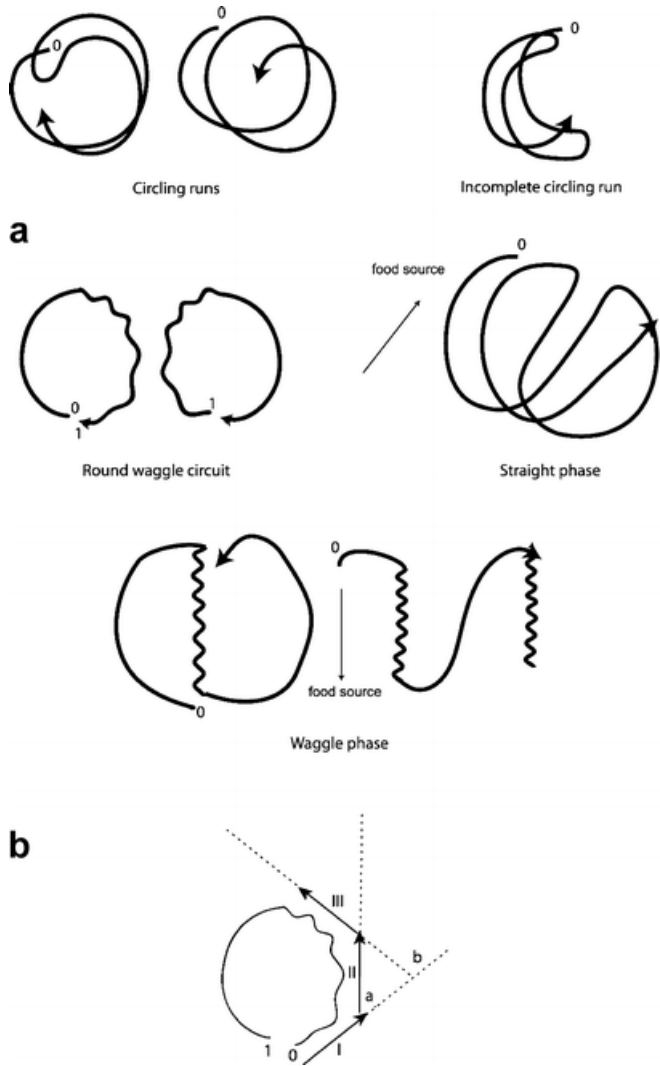
### **Training and data collection**

The colonies were allowed to be in their new locations for a few days. A few bees were trained to a solution of sucrose ( $1 \text{ mol l}^{-1}$ ) and were individually marked once they started making regular

trips. Subsequently the feeder was moved to predetermined distances and dances of the marked bees in the colony were recorded on mini-digital videotapes using a digital camcorder (Sony DCR TRV 7E) at 25 frames  $s^{-1}$ . The recordings at each distance were made in succession, and the time spent at each feeder-distance by the bees was similar. As soon as the desired number of circuits had been recorded (~100), the feeder was moved to a new position. Recording was resumed as soon as all the marked bees had started making regular trips to the new position and were dancing. Efforts were made to record every marked bee that danced for the feeder.

## Data analysis

The digital tapes of dances were replayed at slow speed and dances were categorised as follows. In every dance, we treated each individual dance circuit as a single unit and identified parameters in it for our definitions. Each dance circuit was classified individually as follows (for a schematic representation, see also Fig. 1a): a circling run was defined as a single circuit where the head and thorax of the dancer described a circle of  $360^\circ$  without wagging. In an incomplete circling run the bee failed to describe a complete  $360^\circ$  in her circuit. A waggle phase was defined as that part of the dance circuit where the dancer wagged her body from side to side in a consistent direction throughout the waggle phase (i.e. waggle phase direction did not deviate within the waggle phase by more than  $45^\circ$ ). In an ideal case, the direction of the waggle phase would accurately indicate the direction of the food source. However, such “accuracy” is seen only at long distances and there is usually a large scatter at short distances. During a round waggle circuit the bee wagged her body even as she executed a circuit encompassing  $360^\circ$ , resulting in a waggle phase which consisted of segments whose angles deviated from each other by more than  $45^\circ$  (Fig. 1b). In a straight phase, the dancer executed a “figure of 8” dance but instead of wagging, the body was held rigid.



**Fig. 1a,b** Schematic representations of the different types of dance circuits found in *A. m. carnica* and *A. florea*. 0 indicates the starting point, the *arrowhead* indicates the direction of movement and 1 represents continuation of the circuit. A dancer may execute more than one circuit and the circuits may consist of various types described in detail in the text. **b** A schematic of a round waggler circuit (beginning at 0) with the individual angular components in the waggler phase shown separately by I, II and III (*arrowheads* indicate direction of movement). In this example, I is used as the reference in the direction of the food source and *a* is 52° and *b* is 105° with reference to I

Proportions of circling runs or circuits with waggler phases (regardless of the direction indicated) in all the dances performed by the bees at each distance were calculated and used for the subsequent calculations. Although the other circuit types were also counted and used to calculate relative proportions of waggler phases and circling runs, they were not used in the subsequent analysis as, in general, they constituted a small fraction of the circuit types (~5%) and were not central to our basic question.

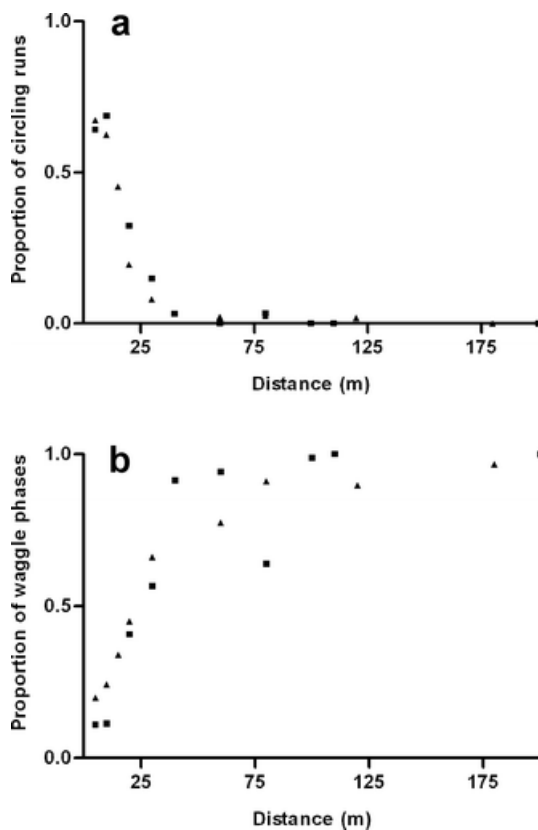
Breakpoint analysis (Jones and Molitoris 1984) is a statistical method to determine the point at which a line changes slope and allows us to test whether the broken line is a significantly better fit to the data than a single straight line.

## Results

It is expected that the proportion of dance circuits that are circling runs should decrease steadily with increasing distance of the food source. Similarly, the proportion of dance circuits that contained waggle phases should increase steadily with increasing distance of the food source. As a first approximation, we fitted the entire data (summarised in Table 1), to a linear regression equation after arcsine transformation (conversion to the  $\sin^{-1}$  value; Sokal and Rohlf 1994). There was a significant linear trend in the decrease in proportion of circling runs with distance (*A. florea*: slope=-0.004,  $r^2=0.47$ ,  $P<0.003$ ; *A.m.carnica*: slope=-0.003,  $r^2=0.36$ ,  $P<0.008$ ) and a significant linear trend in the increase in proportion of waggle phases with distance (*A. florea*: slope=0.009,  $r^2=0.69$ ,  $P<0.0001$ ; *A.m.carnica*: slope=0.006,  $r^2=0.74$ ,  $P<0.0001$ ).

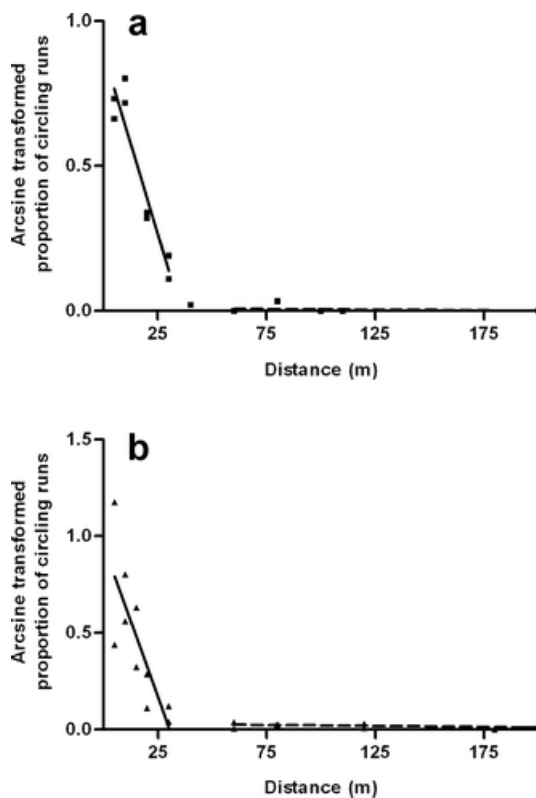
**[Table 1 will appear here. See end of document.]**

However, on closer inspection it became evident that the data (Fig. 2a, b) could be better described by a function consisting of two phases, a linear-phase where the proportion of waggle phases or circling runs changed steadily with distance of feeder, and a saturation-phase where there was not much change with distance. A breakpoint analysis (Jones and Molitoris 1984) showed that the relationship between the proportion of round or waggle phases and distance were better explained by two linear regression equations than a single one (circling runs: *A. florea*:  $r^2=0.96$ ,  $F=75.72$ ,  $P<0.0001$ ; *A.m.carnica*:  $r^2=0.80$ ,  $F=15.81$ ,  $P=0.0003$ ; waggle phases: *A. florea*:  $r^2=0.88$ ,  $F=9.926$ ,  $p=0.0029$ ; *A.m. carnica*:  $r^2=0.88$ ,  $F=7.976$ ,  $P=0.0049$ ).



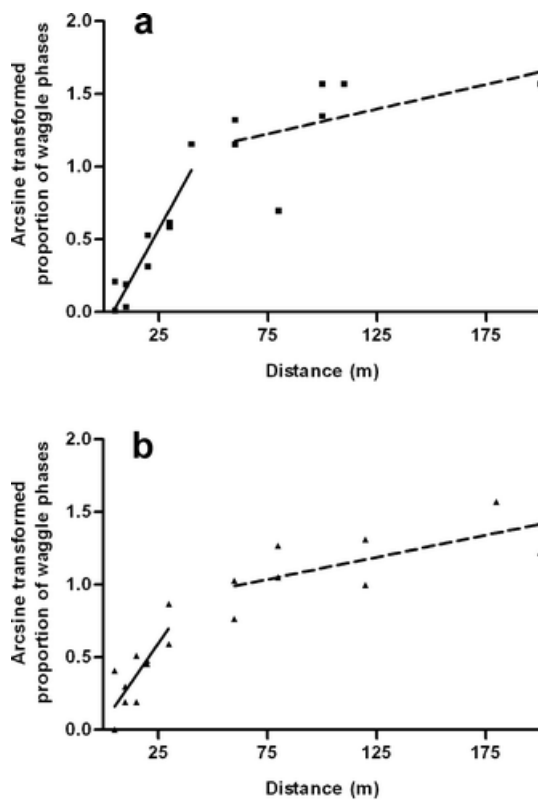
**Fig. 2. a** Proportions of circling runs in the two species studied. Trend lines fitted to the data had significant slopes (*A. florea*: slope= $-0.004$ ,  $r^2=0.47$ ,  $P<0.003$ ; *A. m. carnica*: slope= $-0.003$ ,  $r^2=0.36$ ,  $P<0.008$ ). **b** Proportion of waggle dances in the two species studied. Trend lines fitted to the data had significant slopes (*A. florea*: slope= $0.009$ ,  $r^2=0.69$ ,  $P<0.0001$ ; *A. m. carnica*: slope= $0.006$ ,  $r^2=0.74$ ,  $P<0.0001$ ). Total data set outlined in Table 1. Proportions were calculated from total number of circuits at each distance by all the bees. Circuits were pooled across dances in those cases where a bee contributed more than one dance

In phase 1 (breakpoint: *A. florea*, 34.95 m; *A. m. carnica*, 24.45 m) the decrease in the proportion of circling runs as a function of distance (5–30 m) could be described by a linear regression equation in each species (Fig. 3a, b). The slopes and intercepts of the regression equations were not significantly different across species ( $F$ -test for comparison of slopes,  $P>0.4$ ). Within each species, the two colonies also did not differ from each other significantly ( $P>0.05$ ). In phase 2, the proportion of circling runs did not change significantly with distance (40–200 m) in either species, resulting in a non-significant regression slope in each case. However, this change from phase 1 to phase 2 is likely to be gradual and not as abrupt as might be inferred from the breakpoint.



**Fig. 3** Biphasic representation of the change in proportion of circling runs with increase in feeder distance: **a** *A. florea*, phase 1 ( $y=-0.02x+0.89$ ,  $r^2=0.9$ ,  $n=8$ ,  $P=0.0004$ ), phase 2 ( $y=-0.00005x+0.01$ ,  $r^2=0.039$ ,  $n=7$ ,  $P=0.6$ ); **b** *A. m. carnica*, phase 1 ( $y=-0.03x+0.94$ ,  $r^2=0.64$ ,  $n=10$ ,  $p=0.0058$ ), phase 2 ( $y=-0.00009x+0.03$ ,  $r^2=0.15$ ,  $n=8$ ,  $P=0.34$ ). The slopes and intercepts of the regression equations in phase 1 were not significantly different across species ( $F$ -test for comparison of slopes,  $P>0.4$ ). Similar comparison was not carried out in phase 2, as the slopes were not significant. Data points represent values pooled across individuals in each colony and arcsine transformed. *Solid lines* represent significant trends and *broken lines* represent non-significant trends

Similarly, the increase in the proportion of waggle phases as a function of distance in phase 1 (breakpoint: *A. florea*, 45.55 m; *A. m. carnica*, 40.60 m) could be described by a linear regression equation with significant slope in each species (Fig. 4a, b). The slopes of the regression equations were not significantly different across species ( $F$ -test for comparison of slopes,  $P>0.4$ ). Within each species, the two colonies also did not differ from each other significantly in the slopes ( $P>0.05$ ) but the intercepts were different (*A. florea*:  $P=0.01$ , *A. m. carnica*:  $P=0.03$ ). In phase 2, the proportion of waggle phases did not change significantly with distance in either species, resulting in a non-significant regression slope in each case. Again, it should be noted that this change from phase 1 to phase 2 is likely to be gradual and not as abrupt as might be inferred from the breakpoint.



**Fig. 4** Change in proportion of waggled dances with increase in feeder distance: **a** *A. florea*, phase 1 ( $y=0.02x-0.1$ ,  $r^2=0.87$ ,  $n=9$ ,  $P=0.0002$ ), phase 2 ( $y=0.003x+0.97$ ,  $r^2=0.26$ ,  $n=7$ ,  $P=0.24$ ); **b** *A. m. carnica*, phase 1 ( $y=0.02x+0.05$ ,  $r^2=0.65$ ,  $n=10$ ,  $P=0.0049$ ), phase 2 ( $y=0.003x+0.80$ ,  $r^2=0.44$ ,  $n=7$ ,  $P=0.07$ ). The slopes of the regression equations in phase 1 were not significantly different across species ( $F$ -test for comparison of slopes,  $P>0.4$ ). Similar comparison was not carried out in phase 2, as the slopes were not significant. Data points represent values pooled across individuals in each colony and arcsine transformed. Values were pooled across dances in those cases where a bee contributed more than one dance. *Solid lines* represent significant trends and *broken lines* represent non-significant trends

Thus, the colonies of *A. florea* and *A. m. carnica* used in our experiments did not differ significantly from each other in the relative proportion of circling runs or waggled phases performed as a function of distance. Relative proportion of circling runs was high when the feeder was near the hive as the dancers made mostly or exclusively circling runs. With increasing feeder distance, bees changed over to making more and more intermediate forms of dance and subsequently to elevated numbers of circuits with waggled phases, thus resulting in the relative proportion of circling runs decreasing to nearly zero at around 60 m and the relative proportion of waggled phases increasing beyond 0.5 at 30 m and to higher levels at larger distances.

## Discussion

The colonies of *A. florea* and *A. m. carnica* used in our experiments did not differ significantly from each other in the relative proportion of circling runs or waggle phases performed as a function of distance, or in the manner in which a transition was made from performing predominantly circling runs to performing predominantly waggle phases.

Recent studies on the dance language have also used video technology to study dance behaviour (Kirchner et al. 1988; Jensen et al. 1997; Seeley et al. 2000; Srinivasan et al. 2000; Esch et al. 2001). Use of such technology allows for an increased resolution compared to the original landmark studies by Lindauer (1956) and Boch (1957).

Recent evidence indicates that landscape differences influence distance estimation by honeybees. In future studies it would be of interest to compare different species and races with respect to the waggle duration for a given feeder distance, after controlling for landscape differences to the extent possible.

Selection forces (natural or artificial) are expected to act to a considerable extent on a behavioural trait like the dance language, which largely contributes to the foraging efficiency of all species and races of honeybees. It is known that waggle dances convey more information to dance followers about the food source compared to circling runs, which is reflected in an increased recruitment success (von Frisch 1967). Thus, it cannot be ruled out that the dance behaviour of highly domesticated and actively selected races like *A. m. carnica* has been changing and this change could lead to increasing differences across populations situated in different geographical areas and thus different ecological scenarios. Without sufficient information on the plasticity of the dance language behaviour and linkages at the genetic level with other foraging related traits, this possibility must remain a speculation at present.

It is interesting that there was one aspect in which the colonies differed from each other within each species, namely, the proportion of waggle dances that could be seen at a theoretical distance of 0 m (as can be concluded from the statistically different intercepts of the regression equations for short distances). What this implies is that even though the overall behaviour of the colonies was similar, one colony would show a persistently higher proportion of waggle phases than the other. This supports the speculation that within species, different populations might differ from each other in their dance behaviour, which makes clearly different “dialects” between species and races even less likely.

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**Table 1** Summary of data collected, pooled across colonies

Distance of feeder from hive (m)	<i>A. florea</i>		<i>A. m. carnica</i>	
	Circuits, dances	Bees	Circuits, dances	Bees
5		226, 16	12	289, 17
10		232, 30	12	419, 24
15				323, 18
20		153, 19	7	332, 19
30		201, 17	11	316, 19
40		94, 9	4	
60		180, 23	11	488, 30
80		120, 5	5	312, 15
100		212, 21	11	
110		56, 8	4	
120				283, 13
180				187, 5
200		100, 6	3	52, 4