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Genic control of honey bee dance language dialect

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Abstract Behavioural genetic analysis of honey bee dance language shows simple Mendelian genic control over certain dance dialect differences. Worker honey bees of one parent colony (yellow) changed from round to transition dances for foraging distances of 20 m and from transition to waggle dances at 40 m. Worker bees of the other parent colony (black) made these shifts at 30 m and 90 m, respectively. F_1 colonies behaved identically to their yellow parent, suggesting dominance. Progeny of backcrossing between the F_1 generation and the putative recessive black parent assorted to four classes, indicating that the dialect differences studied are regulated by genes at two unlinked loci, each having two alleles. Honey bee dance communication is complex and highly integrated behaviour. Nonetheless, analysis of a small element of this behaviour, variation in response to distance, suggests that dance communication is regulated by subsets consisting of simple genic systems.

Key words Honey bee · Dance communication · Behavioural genetics · Single-gene effects

Introduction

Honey bees (*Apis mellifera*) rank high as useful experimental subjects that have helped investigators understand behaviour. Most notably, the classic studies of von Frisch and his students (Frisch 1965; Lindauer 1985) described a dance in honey bees that communicates the distance and direction of resources (forage, water, nesting sites etc.) from the nest. This behaviour is so elegant that it is described in most introductions to animal behaviour.

Honey bees also rank high as useful experimental subjects in genetics. In his classic study, Rothenbuhler (1964)

hypothesized that nest-cleaning (hygienic) behavioural differences between two stocks of honey bees were regulated by allelomorphs at two loci. The work used the instrumental insemination of honey bee queens with the semen of single drones to produce colonies of closely related sister worker bees ($r=0.75$ in colonies without inbreeding) (Rothenbuhler 1960). However, minor variation within groups of colonies as classified by Rothenbuhler led Moritz (1988) to question the two-locus – two-allele model. This may illustrate a chief problem in behavioural genetic analysis. Specific functional behavioural genes are difficult to identify because differences in behaviour often overlap due to strong environmental effects, a condition well-documented for hygienic behaviour (Thompson 1964). Beyond Rothenbuhler's (1964) study, work documenting the simple genic regulation of adaptive animal behaviour is rare. Behavioural regulation by genes is mostly inferred from maladaptive mutations that cause disease or from quantitative genetic studies (Whitney 1990; Parsons 1973).

Studying honey bee dance using Rothenbuhler's (1960) unique genetic techniques for evaluating the behaviour of honey bee colonies provides unexplored genetic opportunities. First, variation in honey bee dance forms exists among subspecies of *A. mellifera* as "dialects" (Boch 1956; Frisch 1965). A principal dialect difference is the dance pattern evoked by the distance that resources are from the nest. The common progression of dance pattern forms is from "round" dances through "transitional" dances to "waggle" dances. Round dances indicate a nearby resource and, through sound, (Kirchner et al. 1988) provide some directional information. Transitional dance forms have more directional information and recruit bees to intermediate distances. Waggle dances contain the most precise information and are used when resources are more remote. Within this broad pattern, certain aspects of dance language have been described as being distinctly different between subspecies of *A. mellifera* (Boch 1956; Frisch 1965). Italian honey bees (*A. m. ligustica*) perform round dances for resources up to 10 m distant, varied transitional dances for resources between 20 m and 30 m and waggle dances for

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distances of 40 m or more. In contrast, Carniolan honey bees (*A. m. carnica*) perform round dances for resources at less than 20 m, transitional dances for resources at 30–80 m and waggle dances for 90 m or more. Second, dialect forms evidently are quite environmentally stable. Only the experimental administration of pesticides with pharmacological effects is known to alter dance dialect phenotype (Schricker 1974). Consequently, dance dialect differences might derive from genic differences that could be productively analysed using Rothenbuhler's classic (1960) technique.

One difficulty to this approach is that often individual colonies can display heterogeneous dance dialect phenotypes among their worker bees. To overcome this difficulty, we first sought and found colonies that only displayed homogeneous phenotypes with contrasting dance dialects. We then used these colonies as parents in an F_1 -backcross experiment using Rothenbuhler's (1960) procedures to assess the genic regulation of the dance dialect difference between the selected parents.

Materials and methods

Observation hives

Colonies were placed in glass-walled observation hives for analysis. These hives held three frames holding 13- \times 43-cm combs. One frame of honey with adhering worker bees, two frames of sealed brood with small amounts of honey and pollen and adhering worker bees, and the queen were transferred into observation hives from field equipment. The hives were placed at the study site, and the worker bees were allowed to fly freely for at least 2 days.

Training foragers to feeding stations

Prior to the evaluation of dance behaviour, the worker bees were trained to a movable feeding station within 1 m of the hive entrance. Up to 400 foragers visiting the station were uniquely marked using paint on their thorax and abdomen. After the bees were marked and were foraging frequently at the feeding station, the station was moved to one of the ten feeding station sites located at 10-m intervals to from 10 to 100-m from the entrance of the observation hive. Feeding station sites were on a single vector from the hive entrance because structures and shrubbery interfered with using random vectors. After the bees renewed consistent foraging at each new distance as indicated by frequent foraging visits to the station and little or no dancing at the hive, the station was "closed" by removing all food.

Between 1/2 h and 1 day later, food was returned to the station to initiate an experimental (data collection) period. During an experimental period, an observer recorded the time of arrival and departure of each marked bee. Unmarked bees at the feeding station were caught and killed during both experimental periods and training periods.

When the numbers of marked bees dwindled to the point at which data were difficult to obtain, the remaining marked bees were killed, the feeding station again was moved near the entrance of the hive and a new group of foragers was trained and marked. Thereafter, the feeding station was moved to unstudied experimental distances for further observations.

Observing dancing behaviour

While bees were foraging at the feeding station during an experimental period, a second observer at the observation hive identified

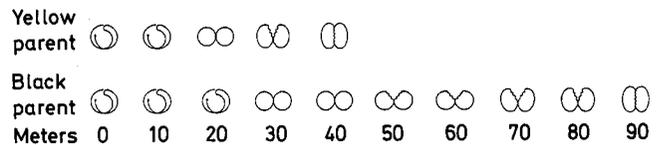


Fig. 1 Dance forms of parental colonies in relation to the distance between the entrance of their hive and the experimental feeding station (adapted from Frisch 1965). The sickle-shaped transitional dances described for Italian bees (Frisch 1965) were not consistently different or common in this study

bees that were dancing and evaluated and recorded the dance form and the time the dance was first observed. Marked variation in dance pattern within colonies (intra-colonial) and even within the performance of a single bee (intra-bee) is well-documented (Esch 1967). We recorded the most "elaborate" dance form (waggle>transition>round) in a bout of dancing because we noticed that bees sometimes start or finish a bout with a less elaborate form. If only one dance form was observed, then at least 10 cycles of the form were required for the dance to be recorded. For a dance with mixed forms, at least 15 dance cycles were observed for the dance to be classified. At least 10 consecutive cycles of the most elaborate dance form were required for the dance to be recorded as the most elaborate form. For other mixed dances, the dances were interpreted as being of the less elaborate form since a clear expression of the more elaborate form was not observed.

We recorded waggle dances when the bees made wagging runs that appeared to be superimposed rather than divergent. We recorded transition dances when runs on diverging straight or semicircular paths ended with typically alternating left and right turns and with semicircular paths usually including 130° of turn and never more than 270° (many graded versions were observed). We recorded round dances when the turning pattern was inconsistent, with semicircular paths ending in hairpin turns having often unpredictable left- or right-hand turns and semicircular paths usually including 360° of turn or more and never less than 270° (Fig. 1).

Mirrors were used to monitor both sides of the observation hive simultaneously. Once noticed, individual dancing foragers were observed closely for characteristics of dance form, dance duration and bee identification. This required that simultaneous dances by other marked bees be ignored. However, when searching for a dance to observe and record at either the beginning of an experimental period or after a dance being observed had ended, we attempted to use the next bee seen dancing.

After each experimental period the two observers (feeding station observer and dance observer) compared records. Only dances by individual bees which had been observed at the feeding station shortly before the dance were used in the evaluations of the colony.

Selection of parents

Parental colonies in this experiment are designated for brevity as "yellow" and "black", which reflects their body colour and suggests *A. m. ligustica* and *A. m. carnica* ancestry, respectively. The Old World subspecies (Italian or Carniolan) of honey bees are probably genically different in many respects from their New World progeny, which have had a history of opportunities for hybridization with many other subspecies (Sheppard 1989). The parental colonies in this study were selected because they had contrasting dance dialects and because they consisted of worker bees that had a uniform dance dialect phenotype. Thirteen candidate parents of yellow "Italian-type" honey bees from the southern United States and 2 candidate black parents of "Carniolan-type" honey bees of a stock bred in isolation in northern Saskatchewan, Canada were evaluated according to these criteria.

In evaluating potential parents we made approximately 51 observations of dances at each experimental distance in order to assure phenotypic uniformity among the worker bees of a colony sired by

several drones. We assumed that ten drones mated with the colony's queen (Page and Metcalf 1982) and that each drone was equally represented in the worker offspring of the colony, and we required a $P \geq 0.95$ that at least 1 daughter of each drone was sampled in efforts to determine if the phenotypes of the colony's workers were homogeneous. The formulas followed Epstein (1977) and were:

$$\binom{10}{K} = \frac{10!}{(10-K)!K!}, \text{ and}$$

$$\sum_{K=0}^9 (-1)^K \binom{10}{K} \left(1 - \frac{K}{10}\right)^n$$

with 10 = the number of subfamilies (drones),

and $\binom{10}{K}$ = the number of combinations of 10 drones taken K at a time.

Production and evaluation of the F₁ generation

Virgin queens and drones were raised from the colonies selected as parents. Instrumental insemination (Harbo 1986) of black or yellow daughter queens with semen from single drones produced 11 colonies having F₁ worker bees: 6 queens were derived from the yellow parent and 5 from the black parent (Fig. 2). The dance dialect of the F₁ workers of each of these colonies was examined using methods similar to those described for evaluating parents.

As a result of using the semen from a single drone for inseminating each queen, the worker bees in each colony had coefficients of relationship of $r=0.75$, and could be expected to have highly homogeneous behaviour. Consequently, the F₁ colonies were evaluated for dance dialect using the dance phenotypes of 10 workers at each distance rather than the 51 at each distance used for evaluating candidate parents.

Production and evaluation of backcross progeny

Results of the evaluation of the F₁ generation (see Results section) supported the hypothesis that the dance form of the Italian yellow parent is genetically dominant to the dance form of the Carniolan black parent. Consequently, the backcross was to the hypothesized recessive black parent (Fig. 2).

Queens of the F₁ generation were raised, and the haploid drones which they produced represented F₁ generation gametes. These drones were used to instrumentally inseminate daughter queens from the presumably recessive black parent (each with the semen from a single drone) to produce a collection of "backcross" colonies (Fig. 2). Twenty-six backcross colonies were evaluated. One backcross colony was lost after it was evaluated in the 0–30 m range. The testing of a colony required a minimum of 1 week but sometimes required more than 1 month. Evaluation procedures were identical to those described for F₁ colonies.

Results

Selection of parents

From the 13 colonies of yellow "Italian-type" honey bees from the southern United States, we found 1 colony of honey bees (yellow parent) that uniformly displayed a distance-related dance language dialect similar to the descriptions of that of Italian honey bees (Boch 1956; Frisch 1965) (Figs. 1, 3a) and chose it as the yellow parent. All of the dances observed shifted from round to transition dances at 20 m, and all shifts from transition to waggle dances occurred at 40 m. The remaining 12 colonies of yellow honey

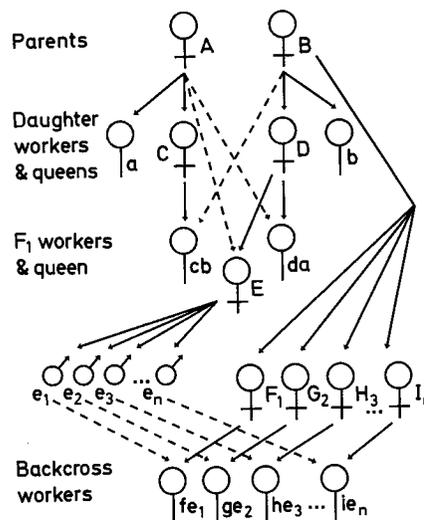


Fig. 2 A pedigree of the colonies tested in the experiment showing the matings that produced them. A solid arrow indicates parentage via an egg, and a dotted arrow indicates parentage via insemination with the semen of a haploid drone. Female symbols A and B represent the yellow and black parent; parent A came from commercial stock in Georgia, USA, and parent B came from commercial stock in Saskatchewan, Canada. Each parent was open-mated to unknown drones. Uncrossed female symbols a and b represent the colonies of worker bees produced by the parents; a and b were evaluated for their dance dialect and for phenotypic uniformity among the workers of each colony. Female symbol C represents 1 of the 6 daughters of parent A that were each instrumentally inseminated with semen from one haploid drone from parent B. Female symbol D represents 1 of the 5 daughters of parent B that were each instrumentally inseminated with semen from one haploid drone from parent A. The instrumentally inseminated C and D queens produced 11 colonies of F₁ worker bees represented by the uncrossed female symbols cb and da. These 11 colonies were evaluated for their dance dialect. Two additional F₁ daughters were reared as queens and are represented by the female symbol E. E queens were used to obtain gametes that segregate from the F₁ generation. The gametes are haploid drones represented by male symbols e₁, e₂, e₃ ... e_n. Since only the haploid drones produced by E queens are involved in the experiment, the mating of E queens is inconsequential. A backcross generation was produced by instrumentally inseminating each of 26 daughters of parent B (represented by female symbols F₁, G₂, H₃, ... I_n) with the semen from one drone of the group e₁, e₂, e₃ ... e_n. These inseminated queens produced colonies of backcross workers represented by the uncrossed female symbols fe₁, ge₂, he₃, ... ie_n. The colonies of backcross workers were evaluated for their dance dialect. This procedure produces colonies of worker bees each of which can be expected to be genetically homogeneous, provided that the original parental colonies have genetically homogeneous workers since haploid drones produce spermatozoa that carry identical copies of the same haploid genome (excepting mutations)

bees displayed heterogeneous dance language dialect phenotypes, which may have reflected heterogeneous genotypes. These colonies were discarded as unsuitable for the experiment.

Of 2 colonies of black "Carniolan-type" honey bees of a stock bred in isolation in northern Saskatchewan, Canada, both uniformly displayed a dialect similar to that of Carniolan honey bees (Boch 1956; Frisch 1965) (Figs. 1, 3a), and we chose one of them as the black parent. All of

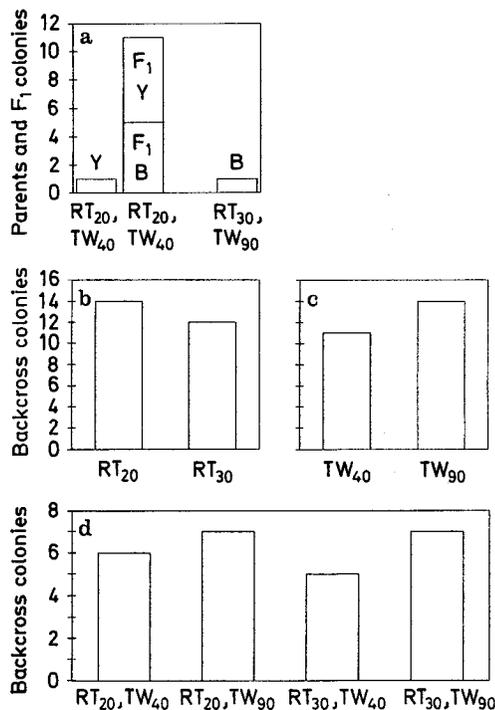


Fig. 3a-d Results of analysis of colonies evaluated for dance dialect: their numbers and phenotypes (RT_{20} =shifting from a round dance to a transition dance after foraging at a training dish 20 m from the hive entrance, a trait of the yellow parent; TW_{40} =shifting from a transition dance to a waggle dance after foraging 40 m from the hive entrance, a trait of the yellow parent; RT_{30} =shifting from a round dance to a transition dance after foraging at 30 m, a trait of the black parent; TW_{90} =shifting from a transition dance to a waggle dance after foraging at 90 m, a trait of the black parent). **a** Parents and F_1 colonies classified according to both the distance resulting in a shift from round to transition dances and the distance resulting in a shift from transition to round dances. ($F_1 Y$ = F_1 colonies derived from yellow queens; $F_1 B$ = F_1 colonies derived from black queens). **b** Backcross colonies classified according to the distance resulting in a shift from round to transition dances. **c** Backcross colonies classified according to the distance resulting in a shift from transition to waggle dances. **d** Backcross colonies classified according to both the distance resulting in a shift from round to transition dances and the distance resulting in a shift from transition to waggle dances

the dancers observed shifted from round to transition dances at 30 m, and all shifts from transition to waggle dances occurred at 40 m.

Although no variation in distance-related dance-type shifts was seen in the parental colonies, minor intracolony and intra-bee variation was observed for parental, F_1 and backcross colonies for unreported training distances, which just preceded those at which we report a dance shift occurred. However, since the object of this study was to examine intercolony variation, we only recorded dance forms at 10-m intervals. Using these distance increments, we observed only consistent intra-colony and intra-bee dance phenotypes. Additionally, some dance language dialect variation remained among the worker bees of experimental colonies. Some worker bees used the "figure-eight" form and some used the sickle-shaped form described for

Carniolan honey bees and Italian honey bees, respectively (Frisch 1965).

In evaluating potential parents we made approximately 51 observations of dances at each experimental distance (mean number of observations per colony per distance=51.6, $SD=2.3$, range=48–57, $n=15$ colonies, experimental distances ranged from 4 to 10) to assure phenotypic uniformity among the worker bees of a colony sired by several drones. In order to assure that dances followed foraging at the feeding station, we only recorded the dances of marked bees that had been observed to forage at the station shortly before they were observed to dance. Periods between foraging and dancing were: $\bar{X}=4.92$ min, $SD=3.2$, range=<1–29, mean number of total dances per colony=788.

Evaluation of the F_1 generation

The F_1 generation was composed of 11 colonies produced by instrumental insemination of 5 black and 6 yellow daughter queens, each with the semen from a single drone of the appropriate parent queen (Fig. 2). The dance dialect of the F_1 workers of all of the F_1 colonies displayed dance dialects with form shifts identical to those of their yellow parent (Fig. 3a). In evaluating F_1 colonies we made about 10 observations of dances at each experimental distance (mean number of observations per colony per distance=10.19, $SD=0.95$, range=7–14, $n=11$ colonies) at which dances occurred shortly after foraging ($\bar{X}=3.8$ min, $SD=2.72$, range=<1–23). The uniform phenotype of the F_1 colonies caused us to conclude that the differences in dance dialect between the parents were under genic control and that the allele (or alleles) present in the black parent was (were) recessive. This conclusion directed the decision to make a backcross to the black parent.

Evaluation of the backcross generation

Of the 26 backcross colonies classified according to the distance at which their foragers shifted from round dances to transition dances, 14 were like the original yellow parent and 12 were like the original black parent (Fig. 3b). Of the backcross colonies, 25 provided data on the distance at which foragers shifted from transition dances to waggle dances: 11 were like the yellow parent and 14 were like the black parent (Fig. 3c). When both transitions in the classification of backcross colonies were used four groups emerged (Fig. 3d): 6 colonies were like the yellow parent for the shift from round to transition dances (shifting at 20 m) (RT_{20}) and like the yellow parent for the shift from transition dances to waggle dances (shifting at 40 m) (TW_{40}), 7 colonies were like the black parent for the shift from round to transition dances (shifting at 30 m) (RT_{30}) and like the black parent for the shift from transition dances to waggle dances (shifting at 90 m) (TW_{90}), 7 colonies were RT_{20} and TW_{90} and five colonies were RT_{30} and TW_{40} (Table 1).

Table 1 Colony types evaluated for dance dialect, their numbers, phenotypes (RT₂₀=shifting from a round dance to a transition dance after foraging at a training dish 20 m from the hive entrance, a trait of the yellow parent; TW₄₀=shifting from a transition dance to a waggle dance after foraging 40 m from the hive entrance, a trait of the yellow parent; RT₃₀=shifting from a round dance to a transition dance after foraging at 30 m, a trait of the black parent; TW₉₀=shifting from a transition dance to a waggle dance after foraging at 90 m, a trait of the black parent), and an interpretation of genotypes that best explains the phenotype (*rt*²⁰, *tw*⁴⁰=dominant allelomorphs derived from the yellow parent regulating the shift from round to transition dances at 20 m and from transition to waggle dances at 40 m, *rt*³⁰, *tw*⁹⁰=recessive allelomorphs derived from the black parent regulating the shift from round to transition dances at 30 m, and the shift from transition dances to waggle dances at 90 m)

Colony type	<i>n</i>	Phenotype	Interpretation of genotype
Yellow parent	1	RT ₂₀ , TW ₄₀	<i>rt</i> ²⁰ , <i>tw</i> ⁴⁰ <i>rt</i> ²⁰ , <i>rt</i> ⁴⁰
Black parent	1	RT ₃₀ , TW ₉₀	<i>rt</i> ³⁰ , <i>tw</i> ⁹⁰ <i>rt</i> ³⁰ , <i>rt</i> ⁹⁰
F ₁	11	RT ₂₀ , TW ₄₀	<i>rt</i> ²⁰ , <i>tw</i> ⁴⁰ <i>rt</i> ³⁰ , <i>rt</i> ⁹⁰
Backcrosses	6	RT ₂₀ , TW ₄₀	<i>rt</i> ²⁰ , <i>tw</i> ⁴⁰ <i>rt</i> ³⁰ , <i>rt</i> ⁹⁰
	7	RT ₂₀ , TW ₉₀	<i>rt</i> ²⁰ , <i>tw</i> ⁹⁰ <i>rt</i> ³⁰ , <i>tw</i> ⁹⁰
	5	RT ₃₀ , TW ₄₀	<i>rt</i> ³⁰ , <i>tw</i> ⁴⁰ <i>rt</i> ³⁰ , <i>tw</i> ⁹⁰
	4	RT ₃₀ , TW ₉₀	<i>rt</i> ³⁰ , <i>tw</i> ⁹⁰ <i>rt</i> ³⁰ , <i>rt</i> ⁹⁰

A goodness-of-fit χ^2 (0.44, 3 *df*, *P*=0.87) indicated that the number in each class did not significantly differ. These results support our interpretations that (1) the difference in dance language dialect between the parents is genically regulated, (2) regulation is by two putative loci each regulating one of the two types of dance form shift and (3) there is no detectable linkage between the loci.

In evaluating backcross colonies we made about 10 observations of dances at each experimental distance (mean number of observations per colony per distance=9.76, SD=1.77, range=5–14, *n*=26 colonies) at which dances occurred shortly after foraging (\bar{X} =4.23 min, SD=2.58, range=<1–21).

Discussion

The experimental outcome permits us to make the interpretation that the two distance-specific changes are regulated by two separate loci (Table 1). For each locus, the allelomorph carried by the yellow parent is dominant to the allelomorph carried by the black parent. The locus *rt* regulates the shift from round dancing to transition dancing and has allelomorphs *rt*²⁰ and *rt*³⁰ regulating shifts at 20 m

and 30 m, respectively. Similarly, the locus *tw* regulates the shift from transition dancing to waggle dancing with allelomorphs *tw*⁴⁰ and *tw*⁹⁰. Further, in the colonies studied, both the yellow parent and the black parent were homozygous for both loci (Table 1).

This study focused on the differences between two colonies. Hence, the identification of two alleles at each of two loci is probably not a complete catalogue of all possible alleles at these two loci or of all the loci regulating dance shifts related to distance. Honey bee dance communication is complex and highly integrated behaviour. Nonetheless, analysis of a small element of this behaviour, the variation in response to distance with specific parental colonies, suggests that dance communication is regulated by subsets consisting of simple genic systems. The evolution of honey bee dance has probably involved the accumulation of many such subsets that have refined the basic genically fixed movements of worker bees that have been successful foragers (Frisch 1965; Lindauer 1961; Esch 1967; Wilson 1971; Michener 1974) or perhaps has even developed from the pre-mating flight dance of drones (Rinderer et al. 1992). Our study documents the existence of the genic regulation of dance dialect differences and supports the view that other elements of dance language that vary less, such as the wagging movement or sound production during dance (Kirchner et al. 1988, Dyer and Seeley 1989), also may be under genic regulation.

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