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Does Imprecision in The Waggle Dance Fit Patterns Predicted by The Tuned-Error Hypothesis?

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Abstract The waggle dance of the honey bee is used to recruit nest mates to a resource, though direction indicated for a resource may vary greatly within a single dance. Some authors suggest that this variation exits as an adaptation to distribute recruits across a patch of flowers, and that, due to the variation's inverse relationship with distance, the shape of the recruit distribution will remain constant for resources at different distances. In this study, we test this hypothesis by examining how variation in the indication of direction and distance changes with respect to distance. We find that imprecision in the communication of direction does not diminish rapidly enough to accommodate an adaptive-error hypothesis, and we also find that variation in the indication of distance has a positive relationship with the distance of a resource from the hive.

Keywords Tuned-error/waggle · dance/distance · communication

Introduction

Evolution is the biological process primarily responsible for the rich diversity of Earth's biota and is accomplished most prominently through natural selection (Darwin 1859). The potential effect of selective pressures on any organism, and the form and function that a trait may realize, can be limited, however, by the current state and evolutionary history of that trait (Gould and Lewontin 1979). Occasionally, students of evolution "atomize" an individual into discrete and independent traits without considering how traits interrelate and influence the evolution of the entire organism. This tendency may lead to ingenious or fanciful explanations of the

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adaptive nature of a trait, and also to the misapprehension that all character states in nature are products of natural selection and exist as optima (Gould and Lewontin 1979).

Of recent interest is the utility of imprecision in the waggle dance of the honey bee. The dance is an adaptation for social recruitment (Sherman and Visscher 2002; Dornhaus and Chittka 2004; Dornhaus et al. 2006) and is used to communicate the location of that resource relative to the position of the sun (von Frisch 1967). The dance works as a ritualized reenactment of the foraging flight, in which the direction flown to a resource, relative to the sun's azimuth, is indicated by the body orientation and movement of the dancing bee relative to "up" on a vertical comb (Fig. 1). This phase of the waggle dance is called a waggle phase. After completing a waggle phase, a dancer returns to its origin via a return phase to perform another waggle phase. Distance is communicated through sound bursts produced during the waggle phase of the dance, the duration of which correlates to the distance of a resource (Wenner 1962; Esch and Kerr 1965; von Frisch 1967).

There is considerable variation, however, in the direction communicated within a single dance (Haldane and Spurway 1954; Wilson 1962; von Frisch 1967; Edrich 1975; Gould 1975; Towne 1985; Towne and Gould 1988; Weidenmüller and Seeley 1999). Though some of this error may be mitigated by the manner in which information from the dance is processed (Tanner and Visscher 2008). The angular difference in the direction between consecutive waggle phases is the divergence angle. Interestingly, the magnitude of the divergence angle has a negative relationship with the distance of a resource from the hive. Some authors contend that the divergence angle has evolved as an adaptation in temperate honey bees to distribute recruits across a resource patch (Wilson 1962; Towne and Gould 1988), and that the relationship between divergence angle and the distance of a resource from the hive represents a tuning to produce a recruit distribution of optimal size that remains constant with distance (Towne 1985; Towne and Gould 1988; Weidenmüller

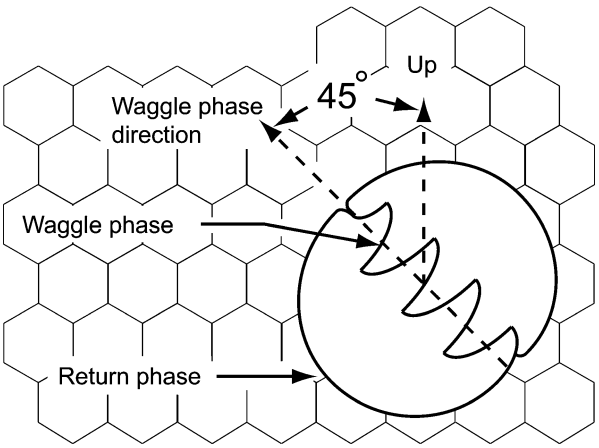


Fig. 1 Waggle dance of the honey bee. In this figure, the waggle phase is oriented 45° to the left of "up" in the hive, communicating that a resource is located 45° to the left of the sun's azimuth. Upon completing this waggle phase, the dancer bee will return to its origin via a return phase, and perform another waggle phase that may indicate a different direction.

and Seeley 1999). A recent study of recruit distributions, however, showed that, at a distance of 250 m from the hive, the distribution of bees was significantly smaller than the imprecision in the dance would predict (Tanner and Visscher 2008). In this study, we test if the imprecision in the indication of distance and direction are sufficient to produce a distribution of recruits that will have the same spatial dimensions as a resource becomes increasingly distant. For a distribution to remain constant with distance, not only must the imprecision in direction decrease, but also the imprecision in distance communication must remain constant. An increase or decrease in variation will alter the size of the distribution.

Materials and Methods

To test what effect the distance of a resource has on the imprecision in the communication of direction and distance, and consequently on the distribution of recruits, we conducted an experiment in which bees were trained to feeders located 200, 400, 600, 800, and 1,000 m from the hive. We recorded the dances and dance sounds of these bees and compared the precision in these dances to models of dance error generated by the tuned-error hypothesis.

Bees and Observation Hive

We used two colonies of bees of mixed European lineage in this experiment; each colony consisted of approximately 2,000 bees. We housed the colonies in observation hives consisting of 2 vertically stacked frames of mixed honey and brood, and wire mesh walls (3 mm mesh size). In order to prevent light from reaching the surface of the hive, which may affect the precision of dancing (Tanner 2003), we placed the observation hives in a darkened, windowless building. Bees entered the hive through a short length of PVC tube that extended from the hive and through the wall of the building. We fitted the interior end of the tube with a wooden wedge so that all bees were directed to the side of the observation hive facing the video camera.

The observation hive and building were located at the Agricultural Experiment Station of the University of California, Riverside amid citrus and Eucalyptus trees, small herbaceous plots of cultivated vegetables, and open fields. There was very little ambient forage available, however, when this experiment was performed.

Training and Data Collection

In this experiment, we trained bees from each colony to feeders located at various distances from the hive by placing a feeder of rich sucrose (2 M) scented with peppermint oil (15 μL/L) directly in front of the colony entrance. Once bees were actively feeding, we moved the feeder 200 m from the hive in small increments. Each bee that arrived at the feeder received a plastic numbered tag, and the dances of these marked bees were video recorded. We included dances consisting of at least 20 consecutive waggle phases in our analysis of dance error.

Dances, illuminated in infrared light, were recorded with a Sony handycam DCR-HC20 digital camcorder on a tripod 0.5 m from the hive. We recorded dance sounds

to the audio track of the digital video tape with a Radio Shack condenser microphone element, first passing the signal through a 15 band graphic equalizer that selectively amplified sounds between 200 and 1,000 Hz. Each bee that successfully performed a dance was collected in a small plastic bag, and placed in a cooler. Once dances from 16 bees were collected, we moved the feeder in small increments 400, 600, 800, and then 1,000 m from the hive repeating the same procedure at each distance.

Video Transcription and Data Analysis

We reviewed the video of dancing bees in 1/6 real time speed using iMovie software, and measured the direction of each waggle phase by tracing the path of the vertex of the dancing bee's head onto a sheet of acetate suspended against a flat screen computer monitor. Next, using a computer program (written by P. K. Visscher U.C. Riverside) that records the x,y coordinates of the pixel at the start and end point of each traced waggle phase, we calculated the angle, relative to "up" in the hive, and the length of each waggle phase. We define the start point of the waggle phase as the point at which the bee began waggling, and the end point as either the point at which waggling stopped, or the point at which the bee began to exit from the waggle phase to the return circuit. Divergence angle was then calculated as the angular difference between consecutive waggle phases, and we calculated the mean divergence angle for each bee in each treatment at each distance. We also calculated the difference between the direction indicated during a waggle phase following a left or right turn and the true direction to the resource. We then calculated a mean "left divergence" and "right divergence", as well as the standard error of the mean, mode, and the range (Table 1 and Fig. 2). We also modeled a divergence angle-to-distance relationship that would result in arcs (i.e. predicted angular distribution of recruits in the field) subtended by the divergence angles of equal size at all distances, and

Table 1 Mean Divergence Angle and Error in Left and Right Waggle Phases

Dance Error					
	200 m	400 m	600 m	800 m	1,000 m
Mean DA	28.67	32.97	22.24	12.79	10.05
Left WP					
Mean difference	15.56	12.85	6.32	8.76	6.17
Standard Err	0.53	0.57	0.37	0.43	0.33
Mode	13	10	1	1	1
Range	43	37	43	29	30
Right WP					
Mean difference	14.9	11.67	6.57	8.33	6.51
Standard Err	0.54	0.49	0.36	0.44	0.36
Mode	13	14	1	2	3
Range	50	34	41	36	33

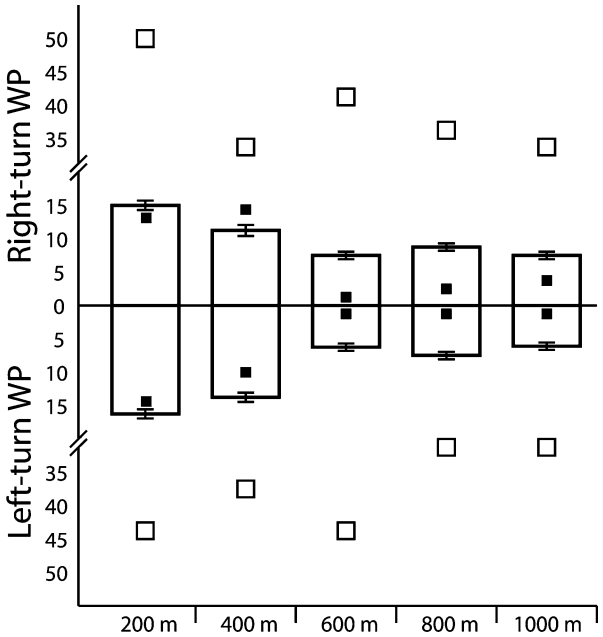


Fig. 2 Analysis of variation in the dance of the honey bee. The bars represent the mean difference between the direction indicated in a waggle phase succeeding a right turn (top) or left turn (bottom) at a given distance. The error bars represent the standard error of the mean, the closed squares represent the mode, and the open squares represent the range, or greatest difference.

compared it with the observed relationship (Fig. 3). The tuned-error hypothesis predicts that the change in divergence angle, or rather the predicted distributions of bees generated from a change in the divergence angle, should track one of the iso-arc-lengths (gray lines).

We quantified the duration of the dancing bees' sound bursts using Raven Lite 1.0 software by measuring the elapsed time between the beginning and end of sound production within a waggle phase. To reduce the background noise, we used the Raven Lite filter to dampen noise that was less than 200 Hz and greater than 1,000 Hz. We then generated an oscillograph for each waggle phase, which we used to measure the duration of each sound burst. To test for an effect of the distance of a resource on the duration of sound bursts, we calculated the mean duration of the sound bursts at each distance, and performed an Analysis of Variance using mean burst duration as the dependent variable, and distance of the resource from the hive as the independent variable. To test for an effect of resource distance on variation in burst duration, we performed a regression analysis in which we regressed the variance in sound burst duration against the distance of the resource from the hive.

Results

Figure 3 depicts the divergence angle to distance relationship that would result in arcs (i.e. the lateral distributions of bees) of equal width at all distances, as a family

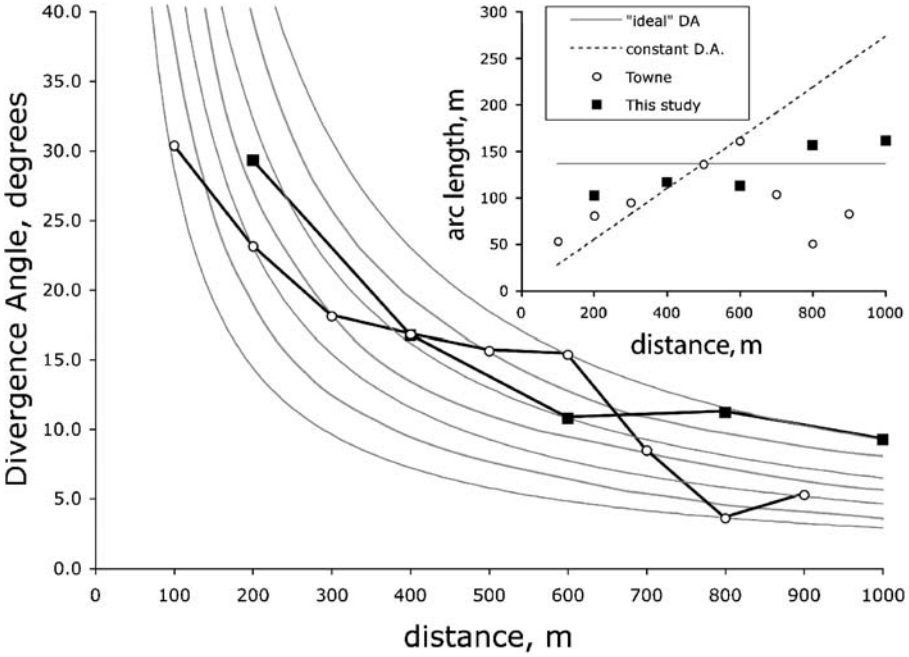


Fig. 3 Decrease in divergence angle with distance graphed against predicted pattern of decrease. Open circles are data taken from Towne and Gould (1988), black squares represent data that we collected.

of iso-arc-length lines (gray lines). The black lines and points represent the data we collected and previously published data of Towne and Gould (1988). The tuned-error hypothesis states that distributions of recruits, resulting from the imprecision in the dance, will have spatial dimensions that are constant despite the distance of a resource. If the imprecision in the dance is sufficient, then the data illustrated on Fig. 3 should follow a single iso-arc-length line. We show, however, that the distributions of bees (black lines), as predicted by dance information, do not track the iso-arc-lengths (gray lines).

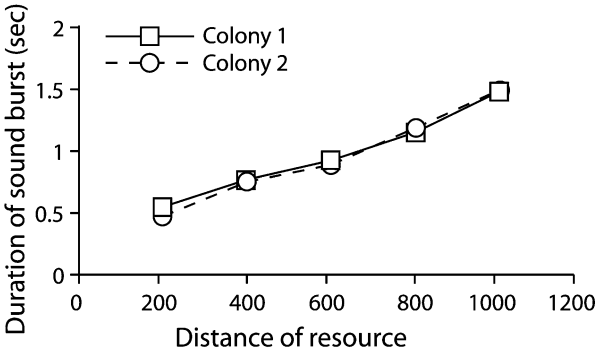


Fig. 4 The effect of resource distance on the duration of sound bursts.

Table 2 Analysis of Variance for the Effects of Distance on Divergence Angle

Source	DF	F	P
Distance	4	158.9	<0.0001
Colony	1	0.00	0.9503
Colony*Distance	4	2.78	0.0282

The graph in the upper right of Fig. 3 plots an arc length (i.e. lateral distribution of bees) to distance relationship produced by holding divergence angle constant at the observed 500 m value (slanted dashed lines), and holding arc length constant with distance (horizontal light line), which represents the relationship predicted by the tuned-error hypothesis. Neither our, nor the data reported by Towne and Gould (1988), fit the relationship predicted by the tuned-error hypothesis of constant arc length with distance. Instead, there are increasing arc lengths (i.e. increasing area over which recruits will be distributed) up to about 500 m, and then steady or decreasing arc lengths.

Figure 4 shows the relationship between sound burst duration and the distance of a resource, and Table 2 contains the results of the ANOVA. These results show that the distance of a resource has a significant effect on sound duration (F=158.9, P< 0.0001), while all other effects were not significant.

The regression of variance in the dance against the distance of the resource from the hive was significant (r^2=0.345, P<0.001), which is consistent with data presented in von Frisch (1967). Figure 5 shows that the variance of sound duration increased with increasing distance.

Discussion

We show that imprecision in dance communication does not fit specific trends predicted by the tuned-error hypothesis. While divergence angle in dances decreases as the distance of a resource increases, it does not decrease rapidly enough to create

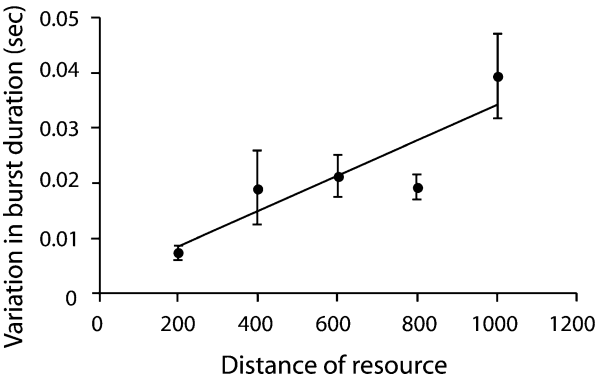


Fig. 5 The effect of resource distance on the variation in sound burst duration.

a spatial distribution of recruits that will remain constant (Fig. 3). Indeed, when resources are located within 500 m from the hive, a model of no change in divergence angle with distance fits the pattern of recruit distribution, as predicted by dance information, better than a model of the tuned-error hypothesis, suggesting that distributions of recruits would increase at a steady rate despite smaller divergence angles. Additionally, we show that the variation in distance communication increases significantly with distance, which may increase the distribution of recruits in the field. We note, however, that while this change in variation is significant, it is not large (Fig. 5). These data suggest that the error in the dance would produce distributions of recruits that noticeably increase in size with the distance of a resource from the hive. This trend was illustrated previously by Towne (1985), who showed a distribution of bees covering an area of 9,920 m^2 at a distance of 100 m from the hive and 20,120 m^2 at 800 m from the hive, though these data were reported to support the tuned-error hypothesis by illustrating distributions of similar sizes at various distances from the hive.

In this study, we tested predicted distributions, and not actual distributions, of recruits against patterns predicted by the tuned-error hypothesis, though our data corroborate previous studies that show that recruit distributions do not fit specific patterns predicted by the tuned-error hypothesis (Towne 1985; Tanner and Visscher 2008). We show here that the imprecision in the communication of direction does not decrease rapidly enough and imprecision in the communication of distance increases too much to generate patterns predicted by the tuned-error hypothesis. We suggest, therefore, that natural selection need not be invoked to explain imprecision in the honey bee dance language, but that it may be more simply explained as an adaptive constraint, and echo the remarks of Williams (1966) on natural selection:

> "This biological principle should be used only as a last resort. It should not be invoked when less onerous principles, such as those of physics and chemistry … are sufficient for a complete explanation."

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