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VISION AS A SENSORY MODALITY IN HONEY BEE (*APIS MELLIFERA*) DANCE COMMUNICATION

By

Mercedes Ramirez

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

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ABSTRACT

VISION AS A SENSORY MODALITY IN HONEY BEE (*APIS MELLIFERA*) DANCE COMMUNICATION

By

Mercedes Ramirez

Communication requires a sender, a receiver and a signal that transmits information. In honey bees (*Apis*), foragers transmit distance and direction information to other bees, but the sensory modality of the signal still remains unclear. There are five candidate sensory modalities: substrate vibration, olfaction, mechanical antennal sensation, audition and vision, but we do not yet know which are most important. In *A. mellifera*, dances are performed in dark cavities, potentially negating a role for vision in dance communication. However, *A. mellifera* dances do sometimes take place in bright light, e.g. on swarms, where vision might be useful. Also, the ancestral dance likely took place entirely on exposed nests, and extant open nesting species have conspicuous visual displays during the dance. Thus, *A. mellifera* may have maintained an ancestral ability to use vision. We tested whether vision is used as a sensory modality by measuring both dancer and follower behaviors under light and dark conditions. The numbers of waggle runs performed by dancers, followers that attended dances, waggle runs followed and follower persistence did not differ significantly between the two light conditions. Despite evidence previously suggesting a difference in follower attraction in light conditions, these results suggest that honey bees do not rely on vision as a sensory modality. It is possible, however, that other measures could reveal a role for vision. That *A. mellifera* does not employ vision in dance communication raises questions about the evolution of the dance signals: the phylogenetic patterns suggest either that the use of vision for dance communication arose independently in open nesting bees, or that the ability to use vision was lost in the ancestors of *A. mellifera*, perhaps when they began using cavities as nests.

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Chapter 1

Introduction

1.1 The honey bee dance language

Communication is generally characterized as the transmission of information from a sender to a receiver via a signal. The honey bee dance language is a prominent example of communication Among non-human animals, first discovered by Karl von Frisch in the early 20^{th} century and most extensively studied in the western honey bee, *Apis mellifera*. The honey bee "waggle" dance is a complex series of stereotypic movements that communicates distance and direction information of food and water sources and nest sites (Von Frisch, 1967; Seeley, 1995). A forager gathers distance and direction information on her trips to the resource, using the sun's azimuth as a reference point. When she returns to the hive, she performs a pantomime of her flight on the hive comb surface, using gravity as a reference, instead of the sun's azimuth (see Figure 1.1).

The waggle dance itself consists of two distinct parts, the waggle run and the return loop. During a waggle run, the dancer will take a single stride and rapidly "waggle" her abdomen, which produces a unique and prominent multimodal signal for other bees in the vicinity (Von Frisch, 1967; Tautz, 1996; Michelsen, 2003). The duration

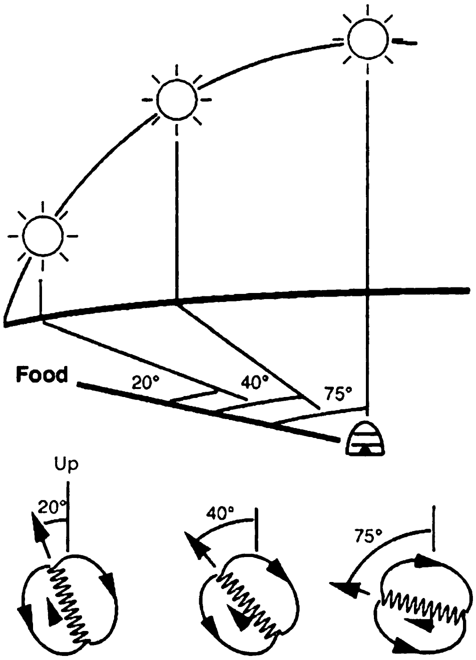

Figure 1.1: Waggle run angles correspond to changes in the angle between the food source traveled to and the sun's azimuth, which changes throughout the day. Modified from Dyer (2002)

of this waggle run can be translated into the actual distance the dancer perceived herself to travel to the source she is indicating, itself influenced by the amount of optic flow feedback she recieves as she flies (Esch, 1967; Dyer, 2002; Von Frisch, 1967). After the waggle run, the dancer travels in an arc to the point where her previous waggle run began, completing one dance circuit. The speed with which the dancer performs the return loop is indicative of her assessment of the relative profitability of the source (Seeley et al., 2000). Dance circuits are often repeated numerous times in succession, called a dance bout, before the dancer leaves to return to the source herself (Von Frisch, 1967). Bees that collect dance information are called followers, as they will often move to follow the dancer as she performs her waggle runs (see Figure 1.2).

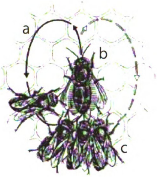

Figure 1.2: Diagram of a waggle run: a) dancer, b followers, c) return loop. Modified from Von Frisch (1967)

1.2 Sensory modalities for transmitting dance information

Although we know much about the function of dance communication in *A. mellifera*, the mechanisms by which waggle dances are performed, and especially how information travels between dancer and follower bees, remain unclear. As a forager dances, other bees in the hive have access to a wealth of information about foraging sites. How are followers accessing this information? At least five candidate sensory modalities have been proposed in *A. mellifera*, including substrate vibration, olfaction, mechanical antennal sensation, audition and vision, but no evidence points definitively to any of these (Esch, 1967; Michelsen et al., 1987; Tautz, 1996; Rohrseitz and Tautz, 1999; Thom et al., 2007; Dyer, 2002). Additionally, we do not know whether the transmission of information is mono- or multi-modal, whether there are any interactions between or among sensory modailites or whether redundant information across multiple modalities allows for flexibility in the face of variable environmental conditions (Dyer, 2002; Grüter and Farina, 2009).

Substrate vibration

During waggle runs, dancers create a weak 200-300 Hz substrate vibration, and given a choice, seem to prefer dancing on open comb, which transmits vibrations better (Tautz, 1996; Nieh and Tautz, 2000). Additionally, dances performed on open comb were more attractive to followers than those performed on sealed comb (Tautz and Rohrseitz, 1998). The substrate vibrations are just within the detection threshold of the subgenual organ (Sandeman et al., 1996). As the vibrations move though the comb, they cause the cell walls to move in response. At a particular distance from the origin of the vibrations, phase reversal of the cell walls occur, such that within a cell, the walls further from the origin are displaced in reverse phase compared to those walls closer to the origin. The result is that the vibration signal is amplified (Tautz et al., 2001). Followers could easily detect this signal by straddling a cell and sensing differences in the positions of pairs of legs as the vibrations move from one end of the cell to another. Indeed, followers located in areas where phase reversal is greatest show the most attraction (Tautz et al., 2001). However, substrate vibrations are clearly not necessary for dance communication: dances for nest sites take place on swarms and are performed on the back of other bees, the movement of which would negate any substrate vibrations. Although perhaps not necessary, substrate vibrations may play a role in attraction of followers to a dancer. Substrate vibrations, then, may not be necessary to successfully transmit dance information, though these results suggest a role in attraction of followers to a dancer. Further experiments are required to determine what role they may play in the transmission of dance information.

Olfaction

Foragers returning from food sources also carry with them floral odors, and this scent influences bee behavior in a number of ways: it can reactivate foragers that have ceased foraging at a food source, and increases the success of locating the proper food source in new recruits. Odorants from the Nasanov gland also serve, in part, to mark successful foraging sites for other foragers (Von Frisch, 1967). Additionally, dancing bees release a unique scent that increases the number of bees that leave the hive (Thom et al., 2007). However, given the rapidity with which dancers vibrate their abdomens, and that this waggling carries in it specific information about distance, it seems unlikely that a odor gradient could transmit this information with sufficient specificity to be useful as a dance communication sensory modality. It appears more likely that dance odorants may be important in attracting followers to dancing bees, but more research is required.

Mechanical antennal sensation

Mechanical antennal sensation, separate from audition, includes tactile contact of follower antennae with the body of the dancer, and using antennae to sense air jets created around a dancer as she dances. Followers seem to prefer to position themselves within ± 30 degrees of dancers' midlines at the rear (Judd, 1995). Follower antennae are buffeted by the rapidly waggling body of the dancer, and in this position, followers may be able to accurately receive both duration of waggling and body angle in relation to gravity, two major components of dance communication, though more experimentation is required to determine how tactile sensations are used (Rohrseitz and Tautz, 1999). A dancing bee also produces a unique set of air jets distinct from air movement caused by the 15 Hz waggling movement and 220 Hz vibration of the wings (Michelsen, 2003). These air jets occur near the abdomen of dancers, and may provide a cue, detectable by the followers' antennae, as to the orientation of the dancer's body. Although air jets have been detected, no experiments have been performed to determine if, or how, followers may perceive and use these potential clues.

Audition

Audition is the favored modality for dance communication. *A. mellifera* dancers create dance 'sounds' by vibrating their wings at around 280 Hz during waggle runs. This causes movement of air particles behind the dancer, know as near-field sounds. The antennae of follower bees can detect these sounds (Towne, 1985; Towne and Kirchner, 1989). A comparison of the dance sounds produced by regular and mutant, small winged, honey bees found that the smaller wings vibrate at a higher frequency, which produced a higher frequency sound, but also reduced the amplitude of the sound produced. When successful follower recruitment rates were compared among bees with normal wings, bees with experimentally clipped wings and mutant small winged bees, recruitment was significantly lower for bees with smaller (either mutant or clipped) wings, suggesting that sounds play an important role in successful follower recruitment (Kirchner and Sommer, 1992). Finally, follower recruitment to an artificial model honey bee dancer was improved when dance sounds were also emitted during waggle runs (Michelsen et al., 1992). Because antennae are used for multiple potential modalities, it may be difficult to disentangle the effects of one modality over another.

Vision

Finally, vision has been generally unstudied as a sensory modality in *A. mellifera*, as they generally nest in dark cavities where vision would be limited. However, dances for nest sites take place in daylight, and the openings of natural cavities vary in size, thus creating relatively lighted situations. In an experiment investigating the importance of tactile contact in follower attraction to dancers, dances performed under artificial lights were more attractive than those performed with infrared illumination (Tautz and Rohrseitz, 1998). Followers appeared to require more tactile contact to become attracted to dances performed in dark conditions, and less tactile contact in light conditions. From this, the authors suggest that vision may have a role in dance communcation, specifically with attraction to dancers. However, to date, no experiments have investigated changes in dancer or follower behaviors in light versus dark environmental conditions, which may indicate whether vision can be used by *A. mellifera*.

1.3 Historical evidence of dance sensory modalities

Because all honey bees use a symbolic dance language to communicate, but particular features and requirements of dancing differs among species, information about dance language mechanisms in other *Apis* species could provide clues on how the *A. mellifera* dance works. Fortunately, the *Apis* genus is small (~10 species), and an older proposed *Apis* phylogeny has been recently confirmed using molecular techniques (Lindauer, 1956; Raffiudin and Crozier, 2007). We can look at trends and correlations related to dance communication across species, and to infer plausible transitions that produced currently observed diversity of species (see Figure 1.3).

A. florea, the dwarf bees, likely represent the extant species that most closely resembles an ancestral *Apis* species. This species forages during the day, and builds nests by wrapping wax comb around a tree branch, creating a nearly horizontal comb surface at the top of the branch. To orient dances, dwarf bees use landmarks or a view of either the sky or the sun as a reference point (reviewed in Dyer 2002). Unlike other *Apis* species, *A. florea* are unable to use gravity to orient their dances on the comb. Waggle runs in this species consist of both dorsal-vental and lateral abdomen movements, and outspread wings, which do not produce near-field sounds (Towne 1985; see Figure 1.4a). The giant bees, *A. dorsata*, are also an open nesting species,

Body movement	lateral & vertical	lateral & vertical	lateral only	lateral only
Nest exposure	open	open	cavity	cavity
Landmarks used	yes	unknown	unknown	yes
Dance sounds	no	yes	yes	yes
Gravity used	no	yes	yes	yes
Dance orientation	'horizontal'	vertical	vertical	vertical
	dwarf bees	**giant bees**	**eastern hive bees**	**western hive bees**
	(e.g. *A. florea***)**	**(e.g.** *A. dorsata***)**	**(e.g.** *A. cerana***)**	**(e.g.** *A. mellifera***)**

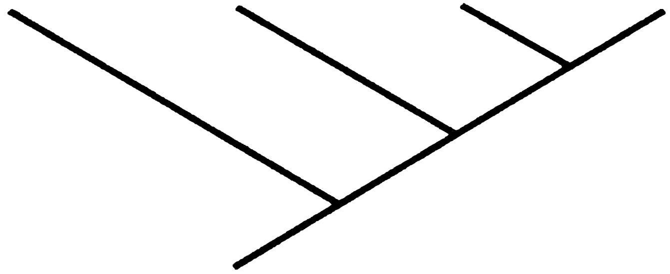

Figure 1.3: Dance communication related traits mapped onto condensed *Apis* phylogeny. Modified from Dyer (2002) and Raffiudin and Crozier (2007)

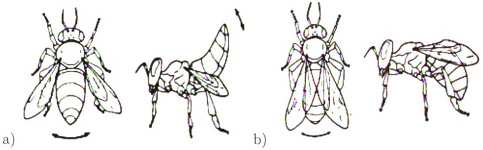

Figure 1.4: Illustrations of a) lateral and dorsal/ventral body waggling and wing positions found in *A. florea* and *A. dorsata*, b) lateral body waggling only and wing positions found in *A. mellifera* and *A. cerana*. Modified from Towne (1985).

but build their comb dangling from tree branches or rock overhangs, creating only vertical comb surfaces. Consistent with comb direction, *A. dorsata* perform dances in the vertical plane, likely using gravity to anchor their waggle dances. No studies have investigated whether giant bees can use landmarks to orient dances. Their waggle runs are similar to those found in *A. florea*; however, unlike *A. florea*, *A. dorsata* do produce dance sounds, particularly when dancing after foraging flights on moonlit nights (Kirchner and Dreller, 1993). In contrast, *A. mellifera* and the closely related eastern hive bee, *A. cerana*, build vertical comb in dark cavities, and use gravity to orient their dances on the comb. Dancers in these species do not perform a dorsal/vental waggle, but only a lateral one during their waggle runs, and produce significant dance sounds by vibrating their closed wings (see Figure 1.4b).

This comparative analysis suggests two trends related to sensory modalities through the evolution of dance communication in *Apis*. The first trend includes light availablilty in the hive environment, using prominent visual signals, and having silent dances, as seen in *A. florea*. The second, as seen in *A. dorsata*, *A. mellifera* and *A. cerana*, is a correlation between dark hive conditions (either at night or from cavity nesting), less prominent visual displays, and sound production during dances. What do these two trends suggest about the sensory modalities used by these species for dance communication? For *A. florea*, silent dances exclude audition, while the generally high environmental light levels, along with visually prominent body and wing displays most strongly support vision as the principle sensory modality. In contrast, a consistently dark nest environment and relatively subdued wing and body displays would seem to exclude vision as a dance sensory modality for *A. mellifera* and *A. cerana*, while the prominent sounds produced during dances in both species supports audition as the most important sensory modality for dance communication. *A. dorsata* seems to hold a unique intermediate position between *A. florea* and *A. mellifera* and *A. cerana* in terms of sensory modalities. This species is not cavity nesting, with light hive conditions, and also has the prominent visual displays seen in *A. florea* dances, both traits suggesting vision. However, unlike other species, *A. dorsata* can forage on moonlit evenings, and during these times have been found to produce more robust dance sounds like *A. mellifera*, which lends support to the position of *A. dorsata* using audition as a sensory modality. No experiments have been performed to determine which sensory modality is used during *A. dorsata* dance communication, but it appears as though *A. dorsata* may be able to use both sensory modalities, depending on environmental conditions.

Thus, a comparative analysis suggests that both *A. florea* and *A. dorsata* use vision as a sensory modality in dance communication (Towne, 1985). We can then ask whether *A. mellifera* have retained this ancestral ability, and can use vision when light is available in the hive environment. Besides evidence from the *Apis* phylogeny, *A. mellifera* dances for nest sites often take place on swarms in daylight conditions, where vision would be a useful modality (Seeley et al., 2000; Dyer, 2002). Finally, some preliminary evidence suggests that light increases the ease of attraction of bees to a dancer, suggesting that follower bees may be able to use vision to find dancers (Tautz and Rohrseitz, 1998). Is vision is a potential sensory modality for transmission of information in the honey bee dance language?

1.4 The focus of this study

Our hypothesis is that *A. mellifera* can indeed use vision as a sensory modality for dance communication in light conditions. Finding evidence of vision use in *A.mellifera* would confirm our assumptions about the ancestral use of vision based on our current understanding of dance language evolution within the *Apis* phylogeny, namely that the *Apis* species ancestral to the whole modern genus relied on visual signals to transmit dance information, and that other sensory modalities evolved later. While adding to our knowledge of dance language evolution within the *Apis* genus, support for vision use in *A. mellifera* would at same time complicate our understanding of the specific dance communication mechanisms in this species by adding evidence for yet another potentially important sensory modality. On the other hand, finding that vision does not seem to be used by *A. mellifera* would not contribute significantly to our knowledge about vision in ancestral *Apis*, but would allow us to rule out vision as a potential sensory modality in *A. mellifera* specifically and focus on others in future research.

To test whether *A. mellifera* can use vision as a sensory modality for dance communication, we applied two global conditions, light and dark, to an observation hive, and measured both dancer and follower behaviors in each condition. We looked for differences between the two light conditions in the number of waggle runs performed by dancers, the number of followers a dancer contacted, the number of waggle runs followed by followers and the following persistence of followers. Differences between light conditions would suggest that vision was being used in some capacity by either dancers or followers.

Chapter 2

Methods

Experiments took place between the summer of 2007 and fall 2008 at Michigan State University, East Lansing, Michigan. A small two frame observation hive of mixed stock *A. mellifera* was housed in a trailer in 2007, and at an MSU bee facility in 2008. Both sites were surrounded mostly by fields; the 2008 site also had numerous larger hives in the area. The hive entrances at both sites faced roughly WNW. Bees were trained to a scented (lemon in 2007, anise in 2008; see Wray et al. 2008) sucrose solution feeder ~500m NNW of the hive entrance, which standardized dances for distance and relative profitability. Trained foragers were individually tagged at the feeder. Because of the presence of other local hives at the 2008 site, all bees that exited the hive were dusted with colored powder to identify and exclude non-dusted individuals from other hives that might have arrived at the feeder by chance. Local weather conditions (temperature, wind speed and wind direction) were measured in 2007 and included as predictors in a general linear model of dancer waggle runs, but did not affect results, and were not collected in 2008.

Table 2.1: Light levels in different natural and experimental environments measured in lux. LED= light emitting diode, CF/FS= compact fluorescent/full spectrum bulbs.

Environment	irradiance (lux)
Dark	0
LED array (2007)	5
CF/FS array (2008)	8
Open nesting conditions	40+
Full sunlight	900+

2.1 Experimental trials

To prepare the hive for experimental trials, a sucrose solution feeder was set out, and marked bees were allowed to forage ad libitum. Unmarked individuals were removed from the feeder and destroyed to minimize recruitment and encourage dancing from marked individuals. Each trial consisted of two 30 minute periods of behavior recording, one period for each light condition. To create a light environment for dancers and followers, we used LED and incandescent lights in 2007, and full-spectrum compact fluorescent lights in 2008 to more closely approximate both the intensity and spectrum of sunlight, measured using a lux meter (see Table 2.1). Dance floor illumination should have been sufficient to allow bees to see one another (see Menzel 1981).

The starting condition was selected randomly at the beginning of the day. Trials began once at least 15 marked bees were actively foraging from the feeder. Digital video of dancers and followers was collected in both light and dark conditions; recording was made possible by an infrared (IR) source on the camera which provided enough illumination for the IR-sensitive camera (Sony Handycam, DCR-HC52). Dancing and following behaviors were captured by aiming the camera at the portion of comb near the hive entrance, where the majority of dances take place. Because forager motivation to continue foraging and dancing was influenced by many variables, including weather, sucrose concentration and time of day, the number of successful trials varied on a day to day basis.

2.2 Video analysis

Prior to video editing and analysis, digital video was imported onto a laptop computer (MacbookPro, Apple, 2006) from digital tapes using Media Edit Pro (MacXware, 2003). Dancers were selected based on the following criteria: dancing bout lasted for at least five waggle runs, dancers performed dancing bouts at least once in each light condition on a given day, and dancers and followers were clearly visible throughout the dancing bout, and not blocked by other bees. Once a dancer was chosen, the number of waggle runs she performed was counted and recorded, as well as the start time of her dancing bout. Followers were chosen using the definition from Wray et al. (2008): bees facing a dancer that were within one bee-length of the dancer, that moved to keep themselves near the dancer, and that followed at least two consecutive waggle runs. These criteria eliminated bees that happened to be near, or passing by a dancer, but were not actually part of the dancing group. To keep of track of followers as they joined and left a dancing group, we marked them digitally. However, because of this, it was impossible to continually track followers once they left dancing groups. Thus, it is likely that some followers are counted multiple times over a number of days. However, this recounting should occur randomly, and so we treated each follower as a different individual. All video was coded using JWatcher (National Institute of Health, 2009).

2.3 Dancer behavior experiments

We predicted that dancers would perform more waggle runs in the dark than the light, attempting to increase the efficacy of transmitting dance information, since it may be harder for followers to locate a dancer in the dark. To test for differences in the mean number of waggle runs performed by individuals in both light and dark conditions, we measured the number of waggle runs individual dancers performed. We used a general linear model to assess the significance of date, weather data (includes outside temperature, wind speed, wind direction), individual dancer identity, light condition and a dancer identity by light interaction on the number of waggle runs performed by dancers in 2007. We log-transformed waggle run values in the model to meet the assumptions of normality and homoscedasticity. We performed a step-wise algorithm to create models from our full model, and compared AIC (Akaike Information Criteria) values to determine the 'best possible' model from variable measured. To specifically determine whether light was a significant influence, we compared the 'best' model, which excluded the light variable, to the same model with the addition of the light variable using ANOVA. We compared waggle run values between summers 2007 and 2008 using ANOVA and found they were not significantly different, so we combined the datasets. We used a paired t-test (n= 31) to compare the mean numbers of waggle runs performed by dancers in light and dark conditions.

We also predicted that dancers would be able to attract more followers in light conditions, as followers would be able to use vision to find dancing groups. We created a general linear model to access the significance of date, dancer identity, number of waggle runs performed by dancers and light condition on the number of followers that were part of a dancing group during individual dancing bouts in 2008. This model met the assumptions of homoscedasticity and normality. We performed a step-wise algorithm to create simpler models from our full model and compared them using AIC values to determine the 'best possible' model. To determine whether light was an important predictor of dance follower number, we used ANOVA to compare the 'best possible' model with one that included light condition.

2.4 Follower behavior experiments

We predicted that followers would be able to follow more waggle runs in the light, since they would be able to use vision as well as other senses to find and follow dancers.We used a general linear model to access the significance of date, dancer identity, the number of waggle runs performed by dancers and light condition on the numbers of waggle runs followers followed in 2008. We log transformed the follower waggle run number to meet the assumptions of homoscedasticity and normality.

Finally, we predicted that followers in light conditions would be able to persist longer in following once they joined a dancing group, again because they would be able to use vision in light conditions. We used only uncensored data, where the start and stop times of following were observed, and analysed the number of waggle runs individual followers followed in both light and dark conditions using a Cox proportional hazard regression model, which gave us following persistence statistics in both light conditions. All statistics were performed in R (R Development Core Team, 2008).

Chapter 3

Results

3.1 Dancer behavior

Do dancers perform more waggle runs in light conditions?

Exploratory statistics

In the summer of 2007, dancers performed an average of 19 (± 12) waggle runs per dancing bout. The range and direction of skew of waggle run data varies between individual dancers (see Figure 3.2). Given this variation between dancers, we expect dancer identity to be an important predictor of the number of waggle runs performed. The most frequent number of waggle runs per dancing bout is skewed towards the left, with the most dancers performing between 10 and 20 waggle runs per dancing bout (see Figure 3.1).

The ranges and skew of waggle run values between Julian calendar days are fairly consistent, but there appears to be a slight decline in the median waggle run value from days later in the season (see Figure 3.3a). Waggle run values plotted against temperature do not reveal any consistent trend; within a temperature waggle runs values tend to be slightly skewed towards lower numbers, but median values hover

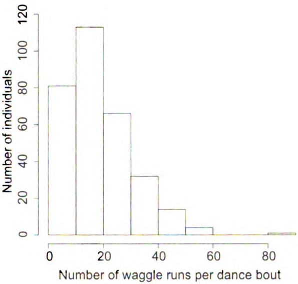

Figure 3.1: Histogram of the number of individuals vs. waggle runs performed in a dancing bout in summer 2007.

around 20 waggle runs (see Figure 3.4). Data for the number of waggle runs performed in light and dark environments appear to have a relatively normal distribution (see Figure 3.3b). There is a slightly wider range of values in the dark condition, and the upper quartile extends further, however, this is likely the result of a one extremely high value for waggle run number. There is no immediately obvious difference between the two distributions, suggesting that light condition will not be a good predictor of waggle run number.

Model selection

We wanted to see if weather variables influenced the number of waggle runs that dancers performed, in addition to the influence of the experimental light variable. From the full model, only dancer identity was a significant predictor of the number of waggle runs that dancers performed (5 out of 28 dancers in 2007, see 3.1). This model accounted for approximately 30% of the variation in dancer waggle run number

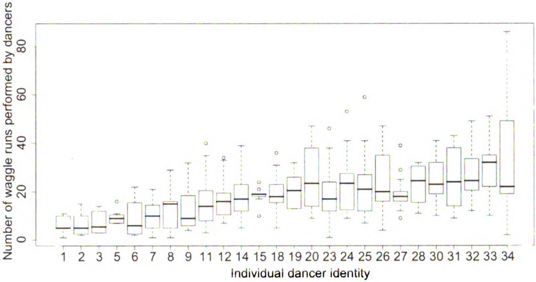

Figure 3.2: Box plot of number of waggle runs performed for each individual dancer in summer 2007. Whiskers indicate highest and lowest points within the 1.5 interquartile range. Open circles indicate data points that lie outside of the 1.5 interquartile range.

($F_{28,282}$=5.54, R^2=0.29, p= <0.001). The final 'best possible' model created from the stepwise algorithm included dancer identity, Julian calendar day, wind speed and headwind ($F_{28,282}$=5.54, R^2=0.29, p= <0.001, see 3.2). Dancer identity and wind speed are significant predictors of waggle run number (ANOVA, $p_D =< 0.001$, $p_W =< 0.03$).

Summary: number of waggle runs performed

The main goal of this study was to assess the influence of light on the number of waggle runs dancers performed. There was no significant difference between a model that included light condition and one without it, suggesting that light condition was not a significant predictor of waggle run number in 2007 (ANOVA, p= 0.58), and the means of waggle runs performed in light and dark conditions in both 2007 and 2008 were not significantly different (paired t-test, t = 0.3568, df = 33, p = 0.72).

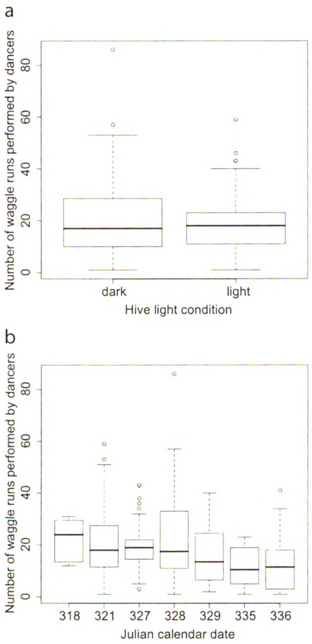

Figure 3.3: Box plots of number of waggle runs performed in a) light and dark conditions, and b) experimental days in summer 2007. Whiskers indicate highest and lowest points within the 1.5 interquartile range. Open circles indicate data points that lie outside of the 1.5 interquartile range.

Table 3.1: General linear model for the number of waggle runs performed by dancers in 2007. Includes estimates of coefficient (β), standard error (SE), 95 % confidence intervals (CI), p-value and significance level (sig level). Stars indicate signifcance level: * = < 0.01, ** = < 0.05, *** = < 0.001.

Response WR	Predictors	β	SE	95% CI	P-value	Sig Level
	Intercept	9.90	6.92	-3.73-23.53	0.15	
	Dancer identity					
	2	-0.02	0.82	-1.82-1.41	0.80	
	3	0.31	0.78	-1.22-1.84	0.69	
	5	0.43	0.76	-1.07-1.93	0.57	
	6	-0.36	0.72	-1.77-1.05	0.62	
	7	0.38	0.80	-1.19-1.97	0.63	
	8	0.05	0.75	-1.43-1.54	0.94	
	9	0.59	0.70	-0.79-1.97	0.94	
	11	0.72	0.72	-0.70-2.15	0.32	
	12	0.93	0.70	-0.44-2.30	0.18	
	14	1.15	0.71	-0.25-2.55	0.11	
	15	1.41	0.84	-0.24-3.07	0.09	
	18	1.27	0.69	-0.10-2.64	0.07	
	19	1.32	0.71	-0.70-2.71	0.06	
	20	1.49	0.70	0.11-2.86	0.03	*
	23	0.38	0.70	-1.00-1.77	0.60	
	24	1.29	0.69	-0.07-2.65	0.06	
	25	1.23	0.69	-0.13-2.59	0.08	
	26	1.07	0.79	-0.48-2.63	0.17	
	27	1.32	0.83	-0.31-2.96	0.11	
	28	1.55	0.76	0.06-3.04	0.42	
	30	1.77	0.79	0.22-3.32	0.03	*
	31	1.09	0.77	-0.42-2.60	0.16	
	32	1.74	0.69	0.38-3.10	0.01	*
	33	1.65	0.70	0.26-3.03	0.02	*
	34	1.46	0.76	-0.31-2.95	0.06	*
	Light condition	0.25	0.77	-1.27-1.77	0.75	
	Julian day	-0.02	0.02	-0.07-0.02	0.31	
	Wind direction	0.001	0.002	-0.002-0.006	0.51	
	Wind speed	0.36	0.20	-0.05-0.76	0.09	
	Temperature	-0.04	0.05	-0.14-0.05	0.37	
	Headwind	-0.28	0.16	-0.59-0.03	0.08	
	Crosswind	-0.20	0.16	-0.51-0.10	0.19	
	Dancer identity x light condition*					
	2 x light	0.46	0.98	-1.47-2.38	0.64	

Table 3.2: 'Best' general linear model for the number of waggle runs performed by dancers in 2007, selected using AIC. Includes estimates of coefficient (β), standard error (SE), 95 % confidence intervals (CI), p-value and significance level (sig level). Stars indicate signifcance level: * = < 0.01, ** = < 0.05, *** = < 0.001.

Response WR	Predictors	β	SE	95% CI	P-value	Sig Level
	Intercept	12.16	4.88	2.55-21.77	0.13	
	Dancer identity					
	2	0.16	0.38	-0.58-0.91	0.66	
	3	0.44	0.41	-0.37-1.25	0.28	
	5	0.58	0.41	-0.23-1.38	0.16	
	6	0.13	0.35	-0.56-0.81	0.71	
	7	0.68	0.40	-0.11-1.46	0.09	
	8	0.55	0.37	-0.19-1.29	0.14	
	9	0.67	0.36	-0.04-1.39	0.07	
	11	0.84	0.34	0.18-1.51	0.01	*
	12	1.10	0.35	0.40-1.79	0.002	**
	14	1.05	0.38	0.30-1.80	0.006	**
	15	1.44	0.38	0.70-2.18	< 0.001	***
	18	1.18	0.37	0.45-1.92	0.002	**
	19	1.28	0.38	0.52-2.03	< 0.001	***
	20	1.46	0.39	0.68-2.23	< 0.001	***
	23	0.86	0.39	0.10-1.62	0.03	*
	24	1.32	0.34	0.65-1.99	< 0.001	***
	25	1.29	0.37	0.57-2.01	< 0.001	***
	26	1.48	0.36	0.78-2.18	< 0.001	***
	27	1.24	0.35	0.54-1.93	< 0.001	***
	28	1.26	0.41	0.45-2.07	0.002	**
	30	1.90	0.39	1.12-2.67	< 0.001	***
	31	1.40	0.35	0.72-2.09	< 0.001	***
	32	1.59	0.37	0.86-2.32	< 0.001	***
	33	1.60	0.40	0.82-2.39	< 0.001	***
	34	1.32	0.37	0.59-2.06	< 0.001	***
	Julian day	-0.03	0.01	-0.06–0.004	0.03	*
	Wind speed	0.13	0.05	0.03-0.22	0.01	*
	Headwind	-0.07	0.04	-0.16-0.02	0.13	

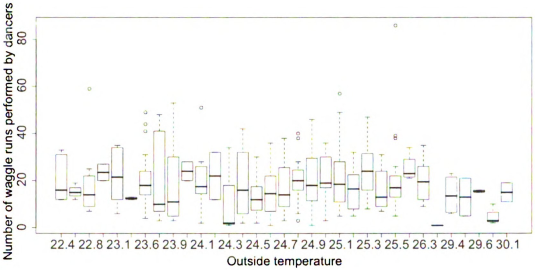

Figure 3.4: Box plot of number of waggle runs performed versus temperatures in summer 2007. Whiskers indicate highest and lowest points within the 1.5 interquartile range. Open circles indicate data points that lie outside of the 1.5 interquartile range.

Do dancers attract more followers in light conditions?

Exploratory statistics

A dancer attracts an average of 13 (± 8) followers during a dancing bout, although the variation between individual dancers is high (see Figure 3.6a). The number of followers is skewed to the left, suggesting that lower followers numbers were more prevalent.(see Figure 3.5). There was no clear trend in the number of followers based on experimental date. The median values differed between days, but the ranges for each day largely overlapped (see Figure 3.6b). Perhaps unsurprisingly, there appears to be a positive correlation betwen the number of waggle runs performed by dancers, and the number of followers they attracted (see Figure 3.7a). The values for the number of dance followers attracted in light and dark are very similar in median value and range, suggesting no significant difference in the number of followers attracted across conditions (see Figure 3.7b).

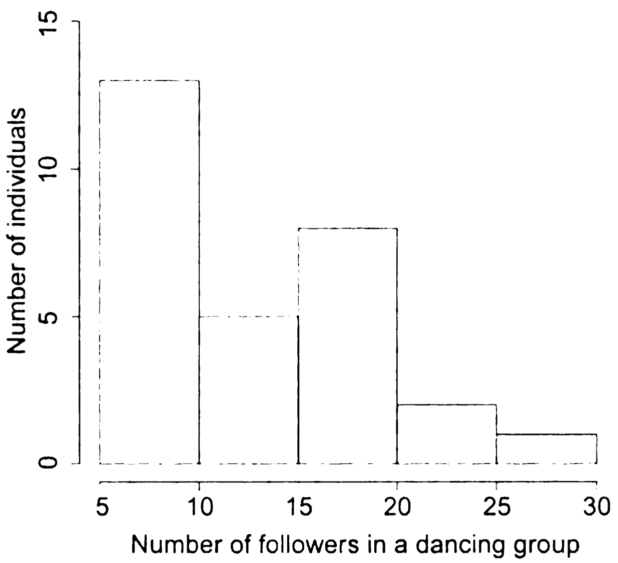

Figure 3.5: Histogram of the frequencies of the number of followers in dancing groups in summer 2008.

Model selection

We created a model for dance follower number that included date, dancer identity, the number of waggle runs performed by dancers, and light condition. Of these variables, date and waggle runs performed by dancers were significant predictors of follower numbers (see Table 3.3). Approximately 55% of the variation in the number of followers attracted to dancing groups was explained by this model ($F_{15,13}$=3.28, R^2=0.55, p = 0.02). The significant predictors from the full model, date, dancer identity and waggle runs performed remained in the 'best possible' model created through stepwise regression (see Table 3.4). The model explained approximately 58% of the variation in follower attraction numbers ($F_{14,14}$=3.78, R^2=0.58, p = 0.009).

Summary: number of followers attracted

Light condition was not a significant predictor of the number of followers attracted to dancers was, as there was no significant difference in the amount of variation

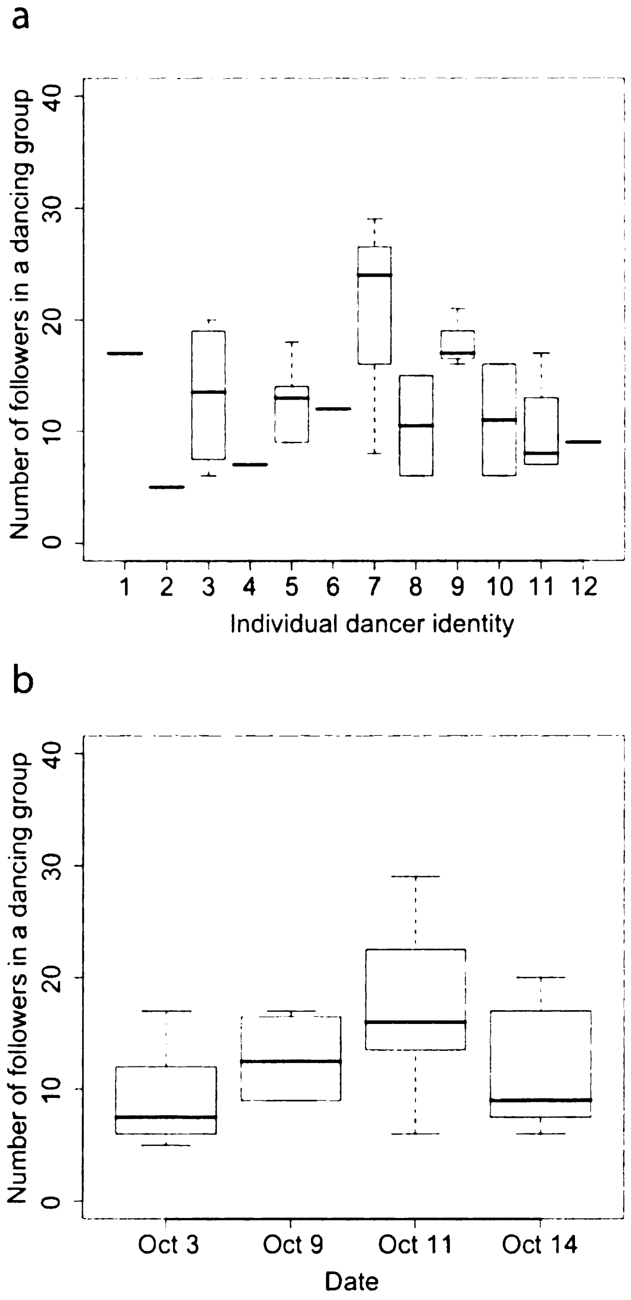

Figure 3.6: Box plots of number of followers in dancing groups versus a) individual dancer identity, and b) experimental date in summer 2008. Whiskers indicate highest and lowest points within the 1.5 interquartile range. Open circles indicate data points that lie outside of the 1.5 interquartile range.

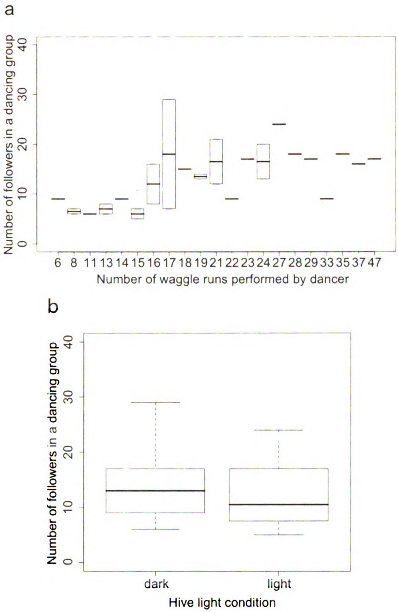

Figure 3.7: Box plots of number of followers in dancing groups versus a) the number of waggle runs performed by dancers, and b) light condition. Whiskers indicate highest and lowest points within the 1.5 interquartile range. Open circles indicate data points that lie outside of the 1.5 interquartile range.

Table 3.3: General linear model for the number of followers attracted by dancers per dancing bout in 2008. Includes estimates of coefficient (β), standard error (SE), 95 % confidence intervals (CI), p-value and significance level (sig level). Stars indicate signifcance level: * = < 0.01, ** = < 0.05, *** = < 0.001.

Response WR	Predictors	β	SE	95% CI	P-value	Sig Level
	Intercept	3.94	6.05	-9.13-17.00	0.53	
	Waggle run number	0.44	0.13	0.16-0.73	0.005	**
	Light condition	0.17	2.01	-4.19-4.51	0.94	
	Date					
	10/09/2008	-1.67	4.19	-10.70-7.38	0.70	
	10/11/2008	8.68	3.37	1.40-15.97	0.02	*
	10/14/2008	3.50	3.49	-4.04-11.04	0.33	
	Dancer identity					
	2	-5.77	6.08	-18.91-7.37	0.36	
	3	-1.15	5.67	-13.40-11.10	0.84	
	4	-0.66	6.42	-14.53-13.21	0.92	
	5	-5.88	5.28	-17.29-5.52	0.29	
	6	2.05	5.45	-9.73-13.83	0.71	
	7	-8.65	6.43	-22.54-5.24	0.20	
	8	-3.29	5.74	-15.70-9.12	0.58	
	9	-2.97	6.81	-17.68-11.74	0.67	
	10	-6.69	5.90	-19.44-6.06	0.28	
	11	-1.11	8.12	-18.65-16.44	0.89	

Table 3.4: 'Best' general linear model for the number of followers attracted by dancers per dancing bout in 2008, selected using AIC. Includes estimates of coefficient (β), standard error (SE), 95 % confidence intervals (CI), p-value and significance level (sig level). Stars indicate signifcance level: * = < 0.01, ** = < 0.05, *** = < 0.001.

Response WR	Predictors	β	SE	95% CI	P-value	Sig Level
	Intercept	4.13	5.38		0.46	
	Waggle run number	0.44	0.13		0.003	**
	Date					
	10/09/2008	-1.64	4.02		0.69	
	10/11/2008	8.60	3.09		0.015	*
	10/14/2008	3.46	3.34		0.32	
	Dancer identity					
	2	-5.79	5.86		0.34	
	3	-1.19	5.45		0.83	
	4	-0.68	6.18		0.91	
	5	-5.88	5.09		0.27	
	6	2.04	5.26		0.70	
	7	-8.66	6.20		0.18	
	8	-3.30	5.54		0.56	
	9	-3.03	6.53		0.65	
	10	-6.74	5.66		0.25	
	11	-1.26	7.63		0.87	

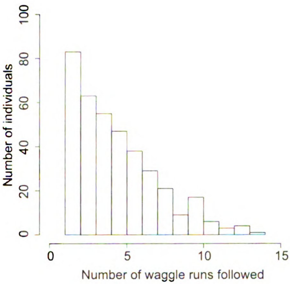

Figure 3.8: Histogram of the frequencies of followers that followed a certain number of waggle runs in 2008.

explained by the model that included light condition (ANOVA, p = 0.87). There was not a significant difference in the mean number of followers attracted in light and dark conditions (t-test, t = -1.17, df = 15.58, p = 0.26).

3.2 Follower behavior

Do followers follow more waggle runs in light conditions?

Exploratory statistics

Follower bees followed an average of 5 (± 3) waggle runs before disengaging from a dancing group. The number of waggle runs followed is left skewed, with most followers following 5 or fewer waggle runs, and frequencies of each number of waggle runs followed tapers off in a regular fashion (see Figure 3.8).

There was not a noticeable trend in the number of waggle runs followed by followers compared to the number of waggle runs performed by dancers, or individual dancer identity. Although the median values differ, they do so seemingly randomly, and the ranges overlap to a great degree (see Figure 3.9). Waggle runs followed do not seem to change significantly based on experimental date (see Figure 3.10a). Both the median values and ranges for the number of waggle runs followed in light and dark are very similar between conditions (see Figure 3.10b).

Table 3.5: General linear model for the number of waggle runs followed by followers in 2008. Includes estimates of coefficient (β), standard error (SE), 95 % confidence intervals (CI), p-value and significance level (sig level). Stars indicate signifcance level: * = < 0.01, ** = < 0.05, *** = < 0.001.

Response WR	Predictors	β	SE	95% CI	P-value	Sig Level
	Intercept	3.94	6.05	-9.13-17.00	0.53	
	Waggle run #	0.44	0.13	0.16-0.73	0.005	**
	Light condition	0.17	2.01	-4.19-4.51	0.94	
	Date					
	10/09/2008	-1.67	4.19	-10.70-7.38	0.70	
	10/11/2008	8.68	3.37	1.40-15.97	0.02	*
	10/14/2008	3.50	3.49	-4.04-11.04	0.33	
	Dancer identity					
	2	-5.77	6.08	-18.91-7.37	0.36	
	3	-1.15	5.67	-13.40-11.10	0.84	
	4	-0.66	6.42	-14.53-13.21	0.92	
	5	-5.88	5.28	-17.29-5.52	0.29	
	6	2.05	5.45	-9.73-13.83	0.71	
	7	-8.65	6.43	-22.54-5.24	0.20	
	8	-3.29	5.74	-15.70-9.12	0.58	
	9	-2.97	6.81	-17.68-11.74	0.67	
	10	-6.69	5.90	-19.44-6.06	0.28	
	11	-1.11	8.12	-18.65-16.44	0.89	

Model selection

Our full model for the number of waggle runs followers followed included the number of waggle runs dancers performed in the dancing bout, the dancer identity, the

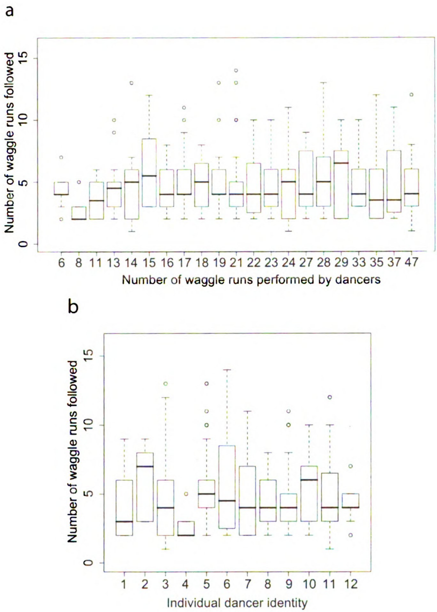

Figure 3.9: Box plots of number of waggle runs followed versus a) the number of waggle runs dancers performed, and b) the individual identity of dancers in summer 2008. Whiskers indicate highest and lowest points within the 1.5 interquartile range. Open circles indicate data points that lie outside of the 1.5 interquartile range.

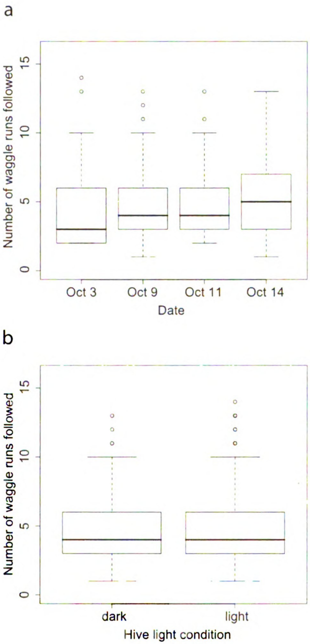

Figure 3.10: Box plots of number of waggle runs followed versus a) experimental date and b) light condition in summer 2008. Whiskers indicate highest and lowest points within the 1.5 interquartile range. Open circles indicate data points that lie outside of the 1.5 interquartile range.

experiment date, and light condition. This model is not very good at explaining variation in the number of waggle runs followed, and none of the variables are significant predictors (see Table 3.5, $F_{16,359}=1.27$, $R^2=0.02$, $p = 0.10$).

Summary: number of waggle runs followers follow

In regards to the effect of light condition on the number of waggle runs followed, there was no significant difference in the amount of variation explained by a model that included light condition and one without it (ANOVA, p=0.29). There was also no significant difference in the mean number of waggle runs performed in light and dark (t-test, t=0.36, df=240.8, p=0.72).

Does following persistence improve for followers in light conditions?

Following persistence, or the probability of a bee continuing to follow once she begins following, remained constant between light conditions and number of waggle runs performed by dancers (see Figure 3.11, Cox proportional hazard, likelihood ratio test= 37.7, df=31, p=0.19).

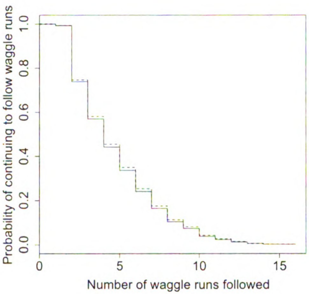

Figure 3.11: Box plot of number of waggle runs performed for each individual dancer in summer 2007. Whiskers indicate highest and lowest points within the 1.5 interquartile range. Open circles indicate data points that lie outside of the 1.5 interquartile range.

Chapter 4

Discussion

In 1967, Karl Von Frisch published "The Dance Language and Orientation of Bees," a collection of the work he began in the 1940's where he proposed that honey bees communicated the location of food sources using a 'dance' language (Von Frisch, 1967). Since that time, intensive research has determined when dance communication is used, how foragers translate and produce dances, what dance communication is used for (Seeley, 1995; Dyer, 2002). The honey bee dance language has become a prominent example of animal communication. In general, communication requires a sender, a receiver and a signal; in the case of honey bees, we still have only a murky understanding of the signal and how it is received and used by the receiver, and thus we have an incomplete picture of the dance language and the workings of honey bee colonies. In this study, we focused on sensory modalities by which honey bee receivers may collect information contained in dance communication.

Based on our knowledge of the dance language in other *Apis* species and known evolutionary relationships among these species, we hypothesized that *A. mellifera* has maintained the ancestral ability to use vision in the dance language, and specifically, that visual signals are used to communicate dance information. To test this hypothesis, we used measures of both dancer and follower behaviors that are important to dance communication, such as the number of waggle runs performed, the number of followers in a dancing group, the number of waggle runs followed, and the persistence of dance followers throughout a dancing bout.

There is modest evidence that followers require more antennal contacts with a dancer to become attracted to and join a dancing group in dark versus light conditions (Tautz and Rohrseitz, 1998). We also know that the number of waggle runs performed by dancing foragers has been previously shown to be influenced by both environmental and individual factors (Von Frisch, 1967; Waddington and Kirchner, 1992; Seeley et al., 2000). Because it may be harder to attract and/or maintain followers in dark conditions, we wondered if dancers altered the number of waggle runs they performed between light conditions to improve the attractiveness of the dance. We measured the number of waggle runs dancers performed in both light and dark conditions and found that they did not respond to changes in light conditions by altering the number of waggle runs they performed within a dancing bout. Thus, dancers do not seem to vary the number of waggle runs as a way to increase follower attraction to dances in dark conditions.

As more waggle runs are performed, dancers contact more potential followers, and followers have increased opportunities to follow dance bouts. Dancers that performed more waggle runs (had longer dancing bouts) had greater numbers of followers than those with shorter dancing bouts. As dancers increase the number of waggle runs they perform, they also increase the opportunities to contact followers that then join the dancing group. Indeed, waggle run number was a significant predictor of the number of dance followers. Because there was no difference in the number of followers in a dancer's group between light conditions, there appears to be no difference in attractiveness of the dance to followers.

This result contrasts with that of Tautz and Rohrseitz (1998), who found that followers in the dark needed more antennal contacts to become attracted to dancers.

The present study is different in two key ways that may explain the difference in results from the Tautz and Rohrseitz (1998) study. First, Tautz and Rohrseitz (1998) defined a follower as a bee who followed at least one waggle run and one return phase, whereas followers in our study needed to follow at least two waggle runs to be counted as followers, as defined by Wray et al. (2008). Thus, some followers that would have been included in earlier study were excluded in this one. We chose to use the Wray et al. (2008) criterion because it was more stringent, and excluded bees that may have passed by a dancer and been momentarily part of the group, but that then moved on. The second key difference is the number of followers used for analysis. Tautz and Rohrseitz (1998) sampled 40 followers, while this study looked at over 300. These methodological differences have likely led to opposing results between the two studies.

This study confirmed earlier reports that followers typically follow five waggle runs consecutively (Von Frisch, 1967). Unexpectedly, we found no correlation between the length of dancing bouts and the number of waggle runs followed by a follower. This result may suggest that followers gain sufficient information to guide their flights within following five waggle runs, and do not need to 'take advantage' of the availability of more waggle runs to increase the accuracy of their interpretation of dance information. We also found no difference in the number of waggle runs followed between light and dark conditions, suggesting that followers are able to follow equally well, regardless of light condition. Thus, vision does not seem necessary to follow waggle runs, and therefore *A. mellifera* followers must use a different sensory modality to receive information from dancers.

Another perspective on follower behaviors in light versus dark is seen in our analysis of follower persistence, which measures how quickly bees drop out of the population following a dancer with each successive waggle run. If followers were using vision to follow waggle runs, we might expect that it would be more difficult to maintain contact with a dancer in darkness. However, we found no difference in follower persistence between the two conditions, indicating that it is not any more difficult for followers to follow waggle runs in the dark.

4.1 Summary and future considerations

None of the behavioral measures used in this study indicate that *A. mellifera* use vision as a sensory modality for dance communication. It remains possible that vision does play a role in the dance language, either in other aspects of behavior not measured in this study, or in follower attraction to dancing groups, as suggested by Tautz and Rohrseitz (1998), although further experiments are necessary. One major concern is whether the light condition was sufficiently bright to allow bees to see each other. The light levels were dark compared to full sunlight in the open, but likely comparable to levels experienced by *A. florea* nests, which are usually shaded by the tree canopy. Brighter conditions also appeared to confuse bees trying to find the hive exit, and so the experimental levels were a compromise between brightness and non-interference in hive activities. That said, we believe the lights were sufficient, and the negative results reported here valid.

These results may also be surprising in light of the evolutionary history of dance communication in the *Apis* genus. Vision is thought to be important in most other *Apis* species, and so a lack of evidence for continued use of vision by *A. mellifera* suggests that they differ from other species not only in their nesting habits, but also in the primary sensory modality that they use in dance communication.

At best, vision is not an important sensory modality for *A. mellifera* dance communication, and may prove to not be used for communication at all. If so, we should look at other sensory modalities as the critical means for dance communication in this species. Just as there are stark differences in how dark the nest environment is across *Apis* species, there are also great differences in the 'noisiness' of dances, with

A. florea having totally silent dances, *A. dorsata* dances being perhaps facultatively noisy , and *A. mellifera* (and *A. cerana*) producing prominent dance sounds. This seems to be the likeliest successful avenue of future investigations, although because of the unique sensory role of follower antennae as mechanosensors, it may be difficult distinguish between audition and tactile sensation.

Understanding the mechanism of information transmission in the honey bee waggle dance is important for a number of reasons. Primarily, knowledge of dance communication mechanisms will shed light on the evolution of the dance language through the *Apis* genus. Based on our current knowledge, the ancestral sensory modality for dance communication is likely vision, much like modern day *A. florea.* If the results of this study are supported by further research, there are two evolutionary possibilities for the lack of vision as a sensory modality in *A. mellifera.* The first is that vision was the ancestral sensory modality, and was subsequently lost by *A. mellifera*, perhaps due to the evolution of cavity nesting. The second possibility is that vision as a sensory modality was not used by ancestral *Apis*, and evolved independently in open nesting species like *A. florea* and *A. dorsata.* Until we more fully understand information transfer in *A. mellifera*, and indeed the other species within the genus, we will not be able to resolve this ambiguity. Additionally, the honey bee dance language is one of the most sophisticated examples of communication in non-human animals. Understanding the mechanisms of this system is vital to determining how, and why, evolution has produced such an advanced system so rarely throughout the animal kingdom. We will be able to compare features of dance language evolution with other advanced systems, like our own, to gain deeper understanding of language and communication more generally.

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