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Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability

Abstract For more than 50 years, investigators of the honey bee's waggle dance have reported that richer food sources seem to elicit longer-lasting and livelier dances than do poorer sources. However, no one had measured both dance duration and liveliness as a function of food-source profitability. Using video analysis, we found that nectar foragers adjust both the duration (D) and the rate (R) of waggle-run production, thereby tuning the number of waggle runs produced per foraging trip (W, where $W = DR$) as a function of food-source profitability. Both duration and rate of waggle-run production increase with rising food-source profitability. Moreover, we found that a dancing bee adjusts the rate of waggle-run production (R) in relation to food-source profitability by adjusting the mean duration of the return-phase portion of her dance circuits. This finding raises the possibility that bees can use return-phase duration as an index of food-source profitability. Finally, dances having different levels of liveliness have different mean durations of the return phase, indicating that dance liveliness can be quantified in terms of the time interval between consecutive waggle runs.

Key words *Apis mellifera* · Communication · Dance language · Foraging · Waggle dance

Introduction

A honey bee colony is capable of deftly deploying its foragers among nectar sources to efficiently extract energy from the surrounding countryside (reviewed in Seeley 1995; Camazine et al. 2000). Flower patches that are large and highly profitable are exploited by many bees, whereas patches that are small or less profitable are worked by fewer bees, perhaps none at all. At the individual level, the adaptive distribution of a colony's foragers comes about through the graded advertisement – by means of waggle dances – of the various nectar sources. The higher the profitability of a particular source, the greater the number of waggle runs produced by a bee working this source when she returns to the hive (Seeley 1986, 1994; Seeley et al. 1991), and because most nectar foragers needing to locate a new work site do so by following several waggle runs of a randomly chosen dance, the greater the dancing for a particular source the larger the stream of newcomers to it (Seeley and Towne 1992; de Vries and Biesmeijer 1999).

One poorly understood part of the mechanisms underlying the adaptive deployment of nectar foragers is how a bee tunes the amount of dancing (number of waggle runs) she does in relation to the profitability of the nectar source that she is visiting. The number of waggle runs produced by a bee upon return to the hive (W, in waggle runs per trip) is the product of two factors:

$$W = DR \qquad (1)$$

where D is the total time spent dancing after the trip (seconds of dancing per trip), and R is the rate of waggle-run production while dancing (waggle runs per second of dancing). Exactly how a dancing bee adjusts D and R to increase W with increasing nectar-source profitability has never been determined. Several authors (Lindauer 1948; Boch 1956; von Frisch 1967; Seeley 1995) have stated that richer sources seem to elicit waggle dances that are both *longer-lasting* (higher D) and *livelier* (a poorly defined property of dances, perhaps related to a higher R) than do poorer sources. These observations suggest that dancing bees adjust both D and R. Surprisingly, though, no one has measured D and R as a function of food-source profitability, so the importance of each factor in adjusting W remains unknown. It also remains unknown what variable(s) in the behavior of a dancing bee underlies the impression that waggle dances vary

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in liveliness. To help resolve these issues, we have made a quantitative description, using video analysis, of the simultaneous tuning of the duration and rate of waggle-run production as a function of sugar-solution concentration. Also, we have used our video recordings to test the hypothesis that differences in rate of waggle-run production underlie the oft-reported differences in dance liveliness.

How bees adjust their dancing in relation to food-source profitability has been examined already for round dances (Waddington 1982; Waddington and Kirchner 1992; Waddington et al. 1998). A worker bee uses a round dance to signal the presence of food in the vicinity of her hive, whereas she uses a waggle dance to indicate the location (direction and distance) of food far from her hive (von Frisch 1967). In one study, Waddington (1982) found that the number of reversals in a round dance (probably analogous to our W for waggle dances), the duration of a round dance (analogous to our D), and the rate of reversals (analogous to our R) all show a positive correlation with food-source profitability. Moreover, he suggested that differences between round dances in liveliness reflect differences in the rate of reversals. Subsequent studies (Waddington and Kirchner 1992; Waddington et al. 1998), however, report that only the rate of reversals has a statistically significant positive correlation with food-source profitability. We will discuss these reports on round dances in the light of our findings on waggle dances.

Materials and methods

We set up an observation hive, trained ten bees to forage at each of two feeders each 350 m from the hive, loaded the feeders with sugar solutions of different concentrations to give the feeders different profitabilities, and video recorded the in-hive behavior of the bees from the two feeders. We then analyzed the video recordings to measure the number of waggle runs produced, the total time spent dancing, and the rate at which waggle runs were produced by each bee each time she returned to the hive. Also, to examine what constitutes dance liveliness, we evaluated the liveliness of each dance and we determined the mean durations of the waggle phase and return phase of each dance.

Study site

The experiments were conducted at the Cranberry Lake Biological Station (44°09′N, 74°48′W), in the Adirondack State Park, Saint Lawrence County, in northern New York State. This study site is surrounded by nearly unbroken forests and lakes, hence there are few natural food sources for bees, making it easy to train bees to forage at feeders.

Apparatus

A colony of approximately 4000 Buckfast honey bees – a strain that has been bred from a cross betweeen Italian bees (*Apis mellifera ligustica*) and English bees (*Apis mellifera mellifera*) (Adam 1987) – was housed in a two-frame observation hive (see Fig. 4.2 in Seeley 1995). To be able to videorecord all dances performed inside the hive, we fitted the hive entrance with a wedge which forced the bees to enter and leave from one side of the comb, and we restricted passage between the two sides of the combs by plugging all side-to-side passageways within 30 cm of the entrance. These measures directed all returning foragers to a well-defined "dance floor" area near the entrance on one side of the hive.

The feeders were designed to provide a sucrose solution with a constant concentration ad libitum for up to 30 bees. They were modeled after the feeders described by von Frisch (1967, his Fig. 2.1; see also Fig. 4.5 in Seeley 1995). Each one consisted of a 50-ml glass jar containing sucrose solution inverted over a slotted Plexiglas plate. This jar-plate combination was placed atop a screened container of anise extract to provide the feeder with scent. Additional scent was provided by mixing 60 µl of anise extract, a 27% (v/v) solution of essential oil in alcohol, into each liter of sucrose solution.

Dances on the vertical comb of the observation hive were recorded with a camera (Panasonic WV-F250B) with docking videocassette recorder (Panasonic AG-7450) equipped with a time-code generator (Panasonic AG-F745). The time-code generator placed an electronic label specifying the time of day (with 1 s precision) and the frame number (30 frames/s) on each frame of a videorecording. The camera's field of view covered all locations where dances were performed in the hive. The videotapes were analyzed using a videocassette player with variable-speed playback (JVC BR-S525U).

Data collection

Each trial of the experiment began by training ten bees to each feeder using a 2.50 mol l^{-1} sucrose solution and standard techniques (Seeley 1995). Both feeders were positioned 350 m from the hive, one to the north and one to the south of the hive. The bees were labeled with paint marks for individual identification. To keep conditions at the two feeders constant, additional bees arriving at each feeder (i.e., recruits) were captured by one of us stationed at each feeder. As soon as there were ten bees visiting each feeder, one feeder was loaded with either a 1.50 mol l^{-1} (trial 1) or a 1.25 mol l^{-1} (trial 2) sucrose solution and the other was maintained with the 2.50 mol l^{-1} solution. Videorecording began after both feeders had been set at the proper level of profitability, the weather conditions had stabilized for the day (both feeders were in the sun, the air was warm enough for flight, etc.), and the bees had had at least 15 min (i.e., sufficient time to complete at least two trips to the feeder) to adjust to their feeder's current level of profitability. The bees' behavior inside the hive was videorecorded steadily for the next 30 min (trial 1) or 45 min (trial 2). At this point, the videorecording was stopped, the concentrations of the sugar solutions in the two feeders were reversed, the bees were given 15 min to adjust to their feeder's new level of profitability, and then the videorecording was resumed for another 30 or 45 min (trials 1 and 2, respectively).

To ensure accurate identification of the bees during playback of the videotapes, one of us pointed to each labeled bee as she entered the hive and announced her identity, which was recorded on the audio track of the videotape. Also, each time a bee produced a waggle dance, we made an assessment of the liveliness of her dance and this too was announced for recording on the audio track. The liveliness of each dance was evaluated by noting its overall vigor and assigning it a value on a three-level scale: lively, moderate, and sluggish. This seems to be what previous authors (Lindauer 1948; Boch 1956; von Frisch 1967; Seeley 1995) have done when judging the liveliness of waggle dances. The video recordings enabled us to compare the dance responses to a richer (2.50 mol l^{-1}) feeder with those to a poorer (1.25 mol l^{-1} or 1.50 mol l^{-1}) feeder. It should be noted that our recordings enabled us to compare the dance responses of bees from the same colony at the same time and in the same place, since the responses to both feeders were witnessed simultaneously and side-by-side in

Table 1 Total amount, duration, and rate of waggle-run production in relation to nectar-source profitability

	Trial 1: 30 June 99			Trial 2: 1 July 99		
	11.00–11.30	N: 2.50	S: 1.50	09.00–09.45	N: 1.25	S: 2.50
	12.15–12.45	N: 1.50	S: 2.50	10.00–10.45	N: 2.50	S: 1.25
Dance variable	2.50 mol l^{-1}	1.50 mol l^{-1}	P	2.50 mol l^{-1}	1.25 mol l^{-1}	P
Waggle runs per trip	9.6 ± 13.5	3.8 ± 6.5	<0.005	7.5 ± 10.3	1.5 ± 3.2	<0.009
Duration of dancing (seconds of dancing per trip)	20.0 ± 18.5	10.3 ± 7.8	<0.001	14.6 ± 13.9	3.6 ± 2.1	<0.015
Rate of waggle-run production (waggle runs per second of dancing)	0.48 ± 0.13	0.37 ± 0.15	<0.001	0.51 ± 0.12	0.41 ± 0.11	<0.005
No. of trips	108	102		135	113	
No. of dances	55	37		47	18	
No. of waggle runs	1040	388		1006	175	

the same observation hive. Furthermore, because we swapped the locations of the richer and poorer feeders in the middle of each trial, we unlinked feeder profitability from feeder location and bee identity. Thus, we could be confident that any differences we might find between dance responses to the richer feeder and the poorer feeder must reflect the difference in profitability rather than some extraneous difference related to bees, time or place of dancing, or feeder location.

Data analysis

The videotapes were analyzed in slow motion. Each time a labeled bee entered the hive we followed her steadily throughout her time inside the hive to determine whether or not she produced a dance. If she did, we noted the starting time and ending time of her dancing, the duration of each pause in dancing that she made (to unload food or to walk about the hive), and the number of waggle runs that she produced (W). We calculated the duration of a dance (D) as the total time spent dancing per return to the hive, i.e., the time interval from start to end of dancing minus any time in between that was spent unloading or wandering; wandering was defined as walking about the hive for more than 4 s. We calculated the rate of waggle run production while dancing (R) as the number of waggle runs produced per return to the hive (W) divided by the time spent dancing per return to the hive (D). Bees that did not dance upon a return to the hive were given values of $W = 0$ and $D = 0$; there was no value of R for these bees. In addition, for each bee that danced upon return to the hive we measured the duration of the waggle phase and of the return phase in each of the first ten dance circuits or, in dances with fewer than ten circuits, as many dance circuits as possible, and then we used these measurements to calculate the mean waggle-phase duration and the mean return-phase duration for the dance produced by this bee during this return to the hive. Waggle-phase and return-phase durations were measured in units of video frames (30 frames/s), thus with a time precision of $1/30 = 0.03$ s. We defined the waggle phase as the portion of a dance circuit during which a bee is making waggle movements with her body. We defined the return phase as the portion of a dance circuit during which a bee is not making waggle movements with her body and instead is circling around to begin her next waggle run (see Fig. 92 in von Frisch 1967). Any return phase that lasted longer than 4 s (because a bee had paused to unload food or walk about the hive) was not used in the analysis of return-phase duration.

All numerical results are given as the mean ± one standard deviation. Statistical tests of the difference between two means were performed using Student's t-test or the Mann–Whitney U-test (used when comparing the mean values of data that were not normally distributed). We also used the chi-square test in a contingency table analysis of the independence of waggle-dance liveliness and food-source profitability.

Results

Tuning duration and rate of waggle-run production

Two trials of our experiment were performed, on 30 June and 1 July 1999. The results, based on analysis of 210 trips recorded in the first trial and 248 trips recorded in the second, are presented in Table 1. We see that in both trials the mean number of waggle runs per trip (W) was much higher for bees visiting the richer feeder than for bees visiting the poorer feeder. We also see that in both trials the higher value of W for the bees from the richer feeder arose because these bees had both a longer mean duration of dancing (D) and a higher mean rate of waggle-run production while dancing (R) than did bees from the poorer feeder.

Analysis of dance liveliness

Was waggle-dance liveliness a function of food-source profitability? Yes, it was: Table 2 shows for both trials the distributions of lively, moderate, and sluggish dances for the richer and poorer feeders. We see that in both trials the large majority of the dances for the richer feeder were rated as lively or moderate, whereas most of those for the poorer feeder were rated as moderate or sluggish. Statistical analysis revealed a signficant ($P < 0.001$, both trials) association between feeder quality and dance liveliness.

Table 2 Waggle-dance liveliness in relation to food-source profitability

Dance liveliness	Trial 1: 30 June 99		Trial 2: 1 July 99	
	2.50 mol l^{-1}	1.50 mol l^{-1}	2.50 mol l^{-1}	1.25 mol l^{-1}
Lively	40	10	31	4
Moderate	10	12	16	8
Sluggish	5	15	0	6
P	<0.001		<0.001	

Table 3 Comparisons of the mean duration of the waggle phase and of the return phase among dances of different liveliness

Dance liveliness	Trial 1: 30 June 99		Trial 2: 1 July 99	
	Waggle phase (s)	Return phase (s)	Waggle phase (s)	Return phase (s)
Lively	0.75 ± 0.10[a]	1.26 ± 0.20[a]	0.79 ± 0.10[a]	1.25 ± 0.22[a]
Moderate	0.81 ± 0.15[a]	1.89 ± 0.29[b]	0.83 ± 0.09[a]	1.96 ± 0.27[b]
Sluggish	0.77 ± 0.13[a]	2.57 ± 0.98[c]	0.80 ± 0.06[a]	2.82 ± 0.45[c]

[a,b,c] Measurements within a column that have different superscripts differ significantly at the $P < 0.01$ level

How do dancing bees alter their dance liveliness? It seemed to us that lively dancers, but not sluggish ones, were "bursting" with desire to produce waggle runs because immediately upon finishing one waggle run they whirled around to start the next one. In other words, it seemed that lively dancers spent less time between waggle runs than did sluggish dancers. To test this idea, we determined the mean waggle-phase duration and the mean return-phase duration for each of the 92 dances in trial 1 and each of the 65 dances in trial 2. As is shown in Table 3, in both trials we found no difference in waggle-phase duration among lively, moderate, and sluggish dances, but we found large and statistically significant differences in return-phase duration among lively, moderate, and sluggish dances. For example, the return-phase duration of sluggish dances was, on average, more than twice that of lively dances.

One might wonder if the differences in mean duration of the return-phase among lively, moderate, and sluggish dancers are a result of the less lively dancers *typically moving slightly more slowly* during their return phases. Alternatively, the differences could be a result of the less lively dancers *occasionally moving much more slowly* during their return phases. These two possibilities are resolved by examining the distributions of return-phase duration for lively, moderate, and sluggish dances. Figure 1 indicates that the first possibility is the actuality. The median values of the three distributions differ widely (1.23 s, 1.70 s, and 2.40 s). Furthermore, more than 97% of the data points for the sluggish dances, for example, are higher than the median value for the lively dances. It seems clear, therefore, that the significantly longer durations of the return-phase in moderate and sluggish dances are not a result of bees dancing moderately or sluggishly occasionally taking long pauses between waggle runs. Instead, we see that moderate and sluggish dancers typically take more time between waggle runs than do lively dancers.

Dance liveliness: an index of food-source profitability?

In Fig. 2 we show the distributions of return-phase duration for dances advertising the 2.50 mol l^{-1} or 1.50 mol l^{-1} feeders on 30 June 99. We see that the two distributions are distinct, as expected given that the bees showed markedly different ($P < 0.001$) rates of waggle-run production for these two feeders (see Table 1). We also see, however, that the two distributions have a broad region of overlap, i.e, the range of return-phase duration of approximately 1.0–3.0 s. Thus, except in the case of a dance with unusually short (<1.0 s) or unusually long (>3.0 s) return phases, measuring the return-phase duration from one circuit of a dance recorded in this experiment would not enable one to know whether the dance represented the 2.50 mol l^{-1} or the 1.50 mol l^{-1} feeder.

Fig. 1 Distributions of return-phase duration for dances classified as lively ($n = 50$ dances), moderate ($n = 22$), and sluggish ($n = 20$). All the dances were recorded on 30 June 99. In making this plot, we used the values of return-phase duration from the first five circuits of each dance. The *three vertical lines* above the data columns denote the median values for each of the three distributions
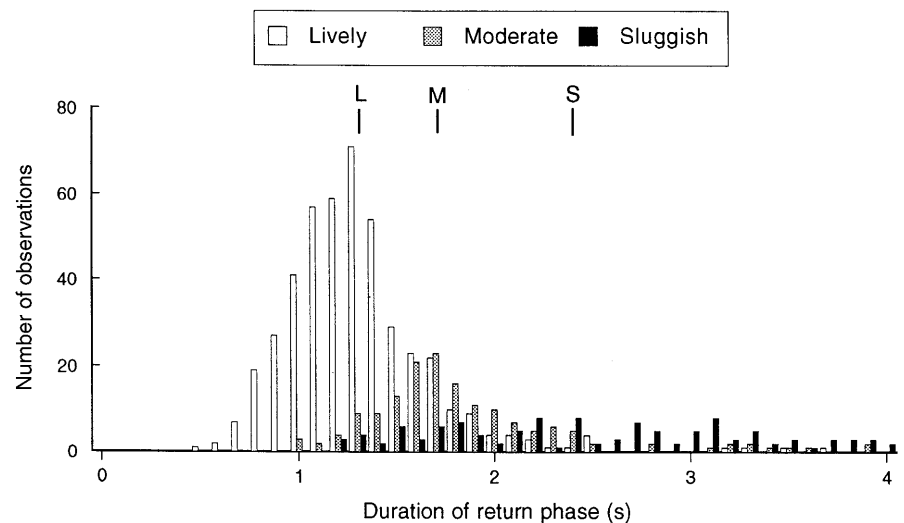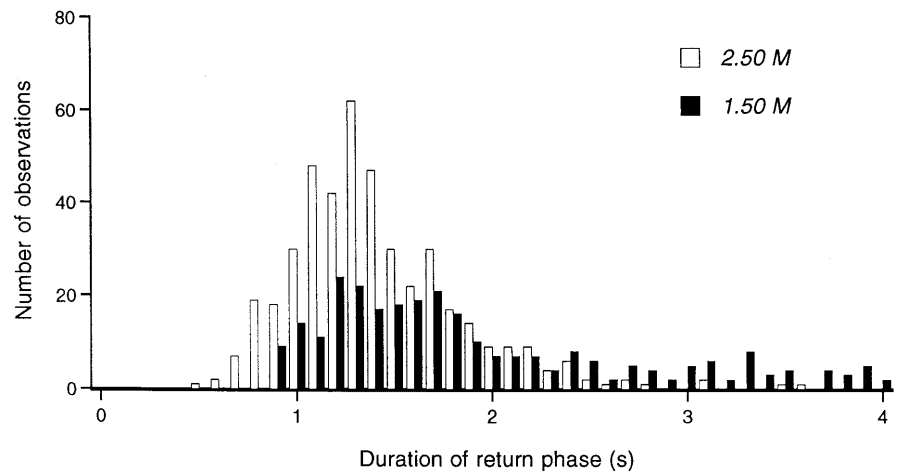
Fig. 2 Distributions of return-phase duration for dances by bees visiting either the 2.50 mol l^{-1} or the 1.50 mol l^{-1} feeder. All dances were recorded on 30 June 99. In making this plot, we used the values of return-phase duration from the first five circuits of each dance

Discussion

The principal result of this study is a better understanding of an important mechanism underlying the adaptive deployment of the nectar foragers in a honey bee colony: how foragers tune the number of waggle runs produced per foraging trip as a function of nectar-source profitability. It is now clear that this tuning involves adjustments in both the duration and the rate of waggle-run production (Table 1), both being increased with increasing nectar-source profitability. It is also now clear that a dancing bee adjusts the rate of waggle-run production by varying the duration of the return-phase portion of her dance circuits while simultaneously holding constant the duration of the waggle-phase portion (Table 3). The constancy of the waggle-phase portion is not surprising because waggle-phase duration codes recruitment-target distance (von Frisch 1967; Michelsen et al. 1992). Finally, this study has confirmed the impression reported by Karl von Frisch and others that richer food sources elicit not only longer-lasting but also livelier waggle dances (Table 2). And since waggle dances having different levels of liveliness have different mean durations of the return phase, it has become clear that liveliness can be quantified, at least in part, in terms of time interval between consecutive waggle runs.

Our results are consistent with the investigations of Seeley (1986, 1994), Seeley and Towne (1992) and Seeley et al. (1991), all of which found that the number of waggle runs produced per foraging trip increases as food-source profitability rises. It is unfortunate, however, that in one of these studies (Seeley and Towne 1992) and in the principal review of this work (Seeley 1995) the number of waggle runs produced per foraging trip (what we now denote by W) was called the "dance duration." This wording is regrettable. For one thing, it obscured the need to examine both the duration (D, in seconds of dancing per trip) and the rate (R, in waggle runs per second of dancing) of waggle-run production as co-variables of a bee's overall dance response (W, in

waggle run per trip). Also, this wording is likely to foster confusion since "dance duration" has now been used to denote both D and W. Future investigators of the waggle dance will need to be mindful of the fact that in Seeley and Towne (1992) and Seeley (1995) the term "dance duration" was used to denote W rather than D.

Our findings on the tuning of *waggle-dance* response in relation to nectar-source profitability are in close agreement with the findings of Waddington (1982) on the tuning of *round-dance* response in relation to nectar-source profitability. Waddington reported a positive correlation between nectar-source profitability and (1) the number of reversals per dance (analogous to our W for waggle dances), (2) the dance duration (analogous to our D), and (3) the rate of reversals (analogous to our R). Moreover, Waddington proposed, just as we have, that what underlies the perception that dances vary in liveliness is variation in the rate of production of dance circuits. Waddington speculated that in round dances a difference in the rate of reversals may "reflect a change in running speed or a change in the size of the dance." For waggle dances, we have shown that the bees change the duration of the return phase, but exactly how the bees accomplish this (by walking faster, by walking a shorter distance, by doing both?) remains unknown.

It also remains unknown why two other studies (Waddington and Kirchner 1992; Waddington et al. 1998) that examined how bees adjust their performance of round dances in relation to food-source profitability did not find a statistically significant positive correlation between round-dance duration and food-source profitability, even though they did find a clear positive correlation between round-dance reversal rate and food-source profitability. Regrettably, neither of these studies reports on the relationship between total number of round-dance reversals and food-source profitability, so it is also unclear whether or not the investigators observed an increase in total number of reversals per round dance with increasing food-source profitability. It seems likely that they did, since if the rate of round-dance reversals is higher following visits to rich sources

relative to poorer sources and the duration of round dances does not differ after visits to the two types of sources, then it follows that the total number of round-dance reversals will differ.

One matter that is now clear is that the classical means (von Frisch 1967) of extracting distance information from waggle dances – by counting the number of waggle runs performed in 15 s – cannot yield precise information. Bees advertising sources equidistant from the hive, but with different profitabilities, will produce different numbers of waggle runs per unit of time as each bee adjusts the return-phase duration of her dance circuits in relation to the quality of her food source. We should instead infer the distance to a bee's food source by measuring the duration of the waggle phase of her dance circuits. Fortunately, this is easy to do with a stopwatch.

Given that the durations of the return phases of a bee's dance circuits are adjusted in relation to the quality of her food source, the question arises whether dance followers can acquire information about the quality of a dancer's food source by measuring the durations of the return phases of her dance circuits, just as dance followers can acquire information about the distance of a dancer's food source by measuring the durations of the waggle phases of her dance circuits. We suggest that some, but probably not much, information about food-source quality can be obtained from measuring the mean return-phase duration of a bee's dance. Our reasoning is as follows. On the one hand, von Frisch (1967, Table 1.3, p 100) has shown that return-phase duration, unlike waggle-phase duration, is little influenced by distance to the food source. For example, as the distance to a rich food source increased from 200 m to 2000 m, the Carniolan bees (*Apis mellifera carnica*) that von Frisch studied increased the *return* phase of their dances by only a factor of 1.04 (from 1.64 s to 1.70 s) but they increased the *waggle* phase of their dances by a factor of 4.62 (from 0.45 s to 2.08 s). The near independence of return-phase duration from food-source distance implies that, in principle, return-phase duration could be a good index of food-source quality. Moreover, we have seen that extremely short (<1.0 s) return phases are exclusively associated with rich (2.50 mol l^{-1} feeder) food sources and extremely long (>3.0 s) return phases are exclusively associated with poorer (1.50 mol l^{-1} feeder) food sources (see Fig. 2). Hence, it appears that dances with extremely brief or extremely long-lasting return phases can be reliably interpreted as indicating highly profitable and less profitable food sources. On the other hand, however, we have seen that both rich and poorer food sources elicit dances with return phases of intermediate duration, from 1.0 s to 3.0 s (see Fig. 2). Hence, unless dance followers can sample multiple return phases within a dance and can determine their mean value, it seems that dances with 1- to 3-s return phases do not provide much information (reduction of uncertainty) about food-source quality. All things considered, therefore, we think that return-phase duration probably is of limited utility as an index of food-source profitability, but we look forward to future investigations on this matter.

More than thirty years ago Karl von Frisch (1967, p 247) provided a clear verbal description of the phenomenon that we have examined in this study: "The profitability of foraging [is] made known by the dancer through the liveliness and duration of her dances, the degree of intensity of their invitation being expressed quantitatively over the entire scale from the dull inception of a single circuit lasting scarcely a second to the stormy mania, lasting for several minutes, of bees that have something especially choice to announce ...". Now, with the aid of videorecording, we have confirmed von Frisch's words. We have found that a bee does indeed tune the amount of dancing she does in relation to food-source profitability by adjusting both the liveliness (i.e., the rate) and the duration of her waggle-run production. Karl von Frisch (1967, p 237) also stated "that [dances] become more vivacious with increasing sugar content is very conspicuous to the observer, but it is not to be defined quantitatively.". On this point we have gone beyond the words of von Frisch by showing that waggle dance liveliness can be defined quantitatively. We have found that the liveliness of a bee's waggle dance is a function of its mean return-phase duration, or in simpler terms, it is a function of how little time a dancing bee spends between consecutive waggle runs.

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