Report

A report involving no dance and rare dance performances of worker honeybees after visiting the feeding station

Takeshi OHTANI¹, Hidetoshi IKENO² and Misako WAKAZONO³

¹ Division of Ecology, Institute of Natural and Environmental Sciences, University of Hyogo / Museum of Nature and Human Activities, Hyogo, Yayoigaoka 6, Sanda, 669-1546 Japan

² School of Human Science and Environment, University of Hyogo, Shinzaike-Honcho 1-1-12, Himeji, Hyogo, 670-0092 Japan

³ Department of Life Science, Faculty of Science, Himeji Institute of Technology, Kouto 3-2-1, Kamigouri-cho, Akou-gun, Hyogo, 678-1297 Japan

Abstract

Several types of dance performance (popular: round dancing and waggle dancing; rare: shaking, tremble dancing, transition dancing and piping) were observed within an observation hive on June 17-24, August 15-17 and November 8-22 in 2001, and September 14-18 in 2003. In the June observation, we observed 3 individuals, 2 of which showed strong persistence in feeding despite the twilight or the rain. For the first time, we observed the replacement from waggle dancing to transition dancing in our nearing trial. In the August observation, we observed *transition dancing*, which was performed horizontally on the passage to the hive entrance. In the November observation, 4 close age-groups were marked with numbered disks in the observation hive for 4 days. Many regular foragers visited the movable feeder at 0.1 to 155 m. The rate of dance appearance (dance performances / flights) was calculated in each individual. The rate in many visitors was considerably lower than that in solo visitors. Waggle dancing was also observed. To our surprise, piping (worker piping) was newly observed. In the September observation in 2003, No.43 also performed piping at the age of 39 and 40 days old. Pink (unknown age) did not perform waggle dancing but transition dancing with over 4 wagglings after reaching the feeder at 155 m. The following 3 points are discussed: (1) shaking or piping as an outlet of excitement in bee flights, (2) the appearance conditions for waggle dancing, and (3) the dance appearance rate during crowded visiting conditions. The last point suggests that dance performances not always appear after a forager has returned from the feeder.

Key words: shaking, tremble dance, round dance, transition dance, waggle dance, worker piping

Introduction

Although most insects are olfactory animals, diurnal honeybees have a considerably developed sense of sight. Recently Srinivasan et al (2000) found out that the odometer of honeybees is visually driven, using a new technique by which dancer bees are made to flow through a narrow tunnel for a food reward. Their results dispelled the old idea of energy consumption for the distance from the hive. They used the occurrence of round and waggle dances as a criterion as to how far a dancer had flown. However, Ohtani (2000, 2002) found that the dance performance of honeybees is not so simple that it can become such a one-dimensional criterion. Successfully using the described tunnel-technique, Esch et al. (2001) reported that dancers could communicate distance measured by optic flow. They followed some of the old procedures by von Frisch (1967) in their data-collection of recruits, taking no notice of the detailed interpretation by Wenner and Wells (1990). Esch et al. (2001)'s control stations were closely monitored for 1.5-2.8 h using as a radius the distance that foragers could reach within

30 s (flight speed: 7.5 m/s, Wenner 1963). They did not mention the influence of wind direction on recruit data, and the binomial distribution (based on the centers of various stations) on recruits without visual or odor cues (cf. Wenner & Wells, 1990:165). Our understanding of the sense of dancers' sight became deeper, but the communication of information through dance remains controversial.

Arnold et al. (2002) reported the intracolonial variability in the dance communication, where only tremble and waggle dances were mentioned as dances that can communicate information to other

nestmates. They followed Seeley (1992)'s idea: a forager uses the tremble dance when it experiences difficulty finding a receiver bee to unload food upon return to the hive. Ohtani (2002) opposed this idea from his detailed observation. Arnold et al. (2002) omitted or ignored mention of *shaking*, *round dancing* and *transition dancing*, which we frequently observed.

Schneider et al. (1998) investigated vibration signal behavior (=shaking) of waggle-dancers in a swarm, and failed to discover its role in the nest-site selection process. They operated under the premise that every behavior invariably has a role; however, some behaviors (such as displacement behaviors) can occur apart from their functions. It is important for behaviors with unknown functions to be described within their context. Ohtani (2000, 2002) reported in detail almost all the processes of his trials, despite his unsuccessful results. The present

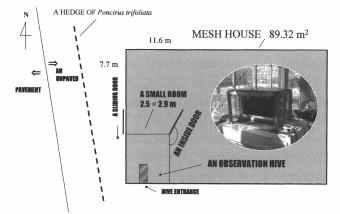


Figure 1. An observation hive in the small room of the Mesh House. All foragers exit through the hive entrance, which is a small hole made by cutting open the mesh wall, and is pasted with a radial mark (see oval photo).

circle means	only one	ODSCI VEI	assigne				
OBSERVATION	BEE(S)	RESULT			OBSERVE	RS	
DAY(S)	OBSERVED	RESULT	T. Ohtani	H. Ikeno	M. Wakazono	T. Koga	OTHERS
May 11,01	Nos.3301,3315		0	0			N. Sasayama
Jun 17,01	No.184	Table 3					
Jun 18,01	Hotaru	Table 4	0	0			Y. Sugano
Jun 21,01	Hotaru	Table 5	0	0			
Jun 22,01	Blue	Table 6	0	0		Ó	
Jun 23,01	Blue	Table 7	0			0	
Jun 24,01	Blue	Table 8	0				H. & M. Ohtani
Aug 15,01	B883		0			0	
Aug 16-17, 01	B883	Table 9	0		0	0	
Nov 6-7, 01			0			0	M. Miyamoto
Nov 8,01	12 indiv.	Figure 3	0	[0	0	M. Miyamoto
Nov 9,01	9 indiv.	Figure 4	0		0	0	M. Miyamoto
Nov 10,01			0				I. Ohtani
Nov 11,01	4 indiv.	Figure 5	•				
Nov 12,01	7 indiv,	Figure 5	0				H. Suzuki
Nov 15,01	No.3104	Table 10					
Nov 16-18, 01	No.3158	Table 10	•				
11 10 00 01	11 0450				<u> </u>		1

Table 1. Observer(s) assigned to each observation day. Ablack circle means only one observer assigned.

paper also fully describes any possibly relevant observational data, detailing the situation and behaviors of dance performances of honeybees.

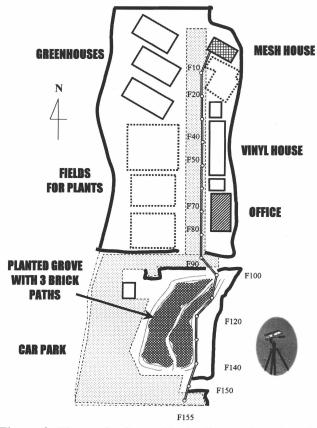


Figure 2. The track of movable feeding stations (small circles) at the Gene Farm and the car park of our Museum. F100 denotes the feeder at 100 m. Only one feeding station was opened far from the hive. The dotted area is a surface paved with concrete. The heavy line denotes a hedge of ookanamemochi (*Hotinia serratifolia*, Rosaceae). There is an open road paved with concrete on the north and east sides, and a dense thicket on the south and west sides of this experimental field.

	BEHAVIOR PATTERN	TYPE	CODE	SHAPE OF TURNING	NO. WAGGING	REFERENCES
1)	Dancing		DA			Ohtani (2000)
la)	Round dancing		Da'	circle	0	von Frisch (1967); Ohtani (2000)
1b)	Waggle dancing		Da "	double half circle	4+	von Frisch (1967); Ohtani (2000)
1c)	Transition dancing		Da'			von Frisch (1967); Ohtani (2000)
<u>´</u>	without tail-wagging		Da ^{t0}	eight	0	von Frisch (1967); Ohtani (2000)
	with 1 or 1.5 tail-waggings		Da ^{tl}	eight	1, 1.5	von Frisch (1967); Ohtani (2000)
	with 2 or 2.5 tail-waggings		Da ¹²	eight	2, 2.5	von Frisch (1967); Ohtani (2000)
	with 3 or 3.5 tail-waggings	normal	Da ¹³	eight	3, 3.5	von Frisch (1967); Ohtani (2000)
	with over 4 tail-waggings	vigorous	Da ¹⁴	eight	4+	Ohtani (2002); the present report
2)	Tremblle dancing		TD			Seeley (1992)
2a)	Tremble walking		Td ^w	nothing	0	Seeley (1992); Ohtani (2000)
2b)	Tremble running		Td'	nothing	0	Ohtani (2000)
3)	Shaking		Sh /w	nothing	0	Haydak (1929); Ohtani (1994)
4)	Piping		Pi	nothing	0	Ohtani & Kamada (1980); Ohtani (199

Table 2. Dance performances used in the present report.

Materials and Method

Impure Italian colonies (*Apis mellifera ligustica*), such as those usually sold in the Japanese market, were used in our observations. Newly emerged workers were marked with numbered disks and introduced into our observation hive, which was placed in the small room of the Mesh House (Figure 1) at the Gene Farm of the Museum of Nature and Human Activities, Hyogo in Sanda City (Hyogo Pref.).

Our observations were carried out in the Mesh House $(7.7 \times 11.6 \text{ m})$ used in the earlier study (Ohtani, 2002). It is a greenhouse with no glass but meshed walls and a roof. Then, we used the observation hive (Ohtani, 2002), which was placed in the small room (roofed with corrugated sheets) of the Mesh House (Figure 1) and on a metal vessel filled with water, the temperature of which was controlled by an electric heater.

Usually 2 observers were assigned to the feeding station and the observation hive. The observers communicated with each other via transceivers. Table 1 shows the schedule of observers for each observation day.

The food in the feeder was a mixture of honey diluted with the same quantity of water. The mobile feeding station was regularly moved, from 0 to 155 m (Figure 2).

Observations were carried out in 4 blocks: June, August and November in 2001, and September in 2003. These blocks are assigned in separate sections in the Results with Short Comments, after the first section. Detailed procedures are described in each section.

Results with Short Comments

1. Dance performances described by Ohtani (2000, 2002)

This report was based on the descriptions by Ohtani (2000, 2002). For convenience, a summary of dance performance types is shown in Table 2. The differences from the table of Ohtani (2002) include the deletion of definition by position and movements, the addition of Da^{t4} , promoted from the vigorous type of Da^{t3} , the modification of the definition of Da^{t3} , and the supplement of *piping* (*Pi*) newly observed on Nov. 19 (cf. Table 11).

2. Three foragers in the June observation

Our observation of dance performances started on May 11, 2001. Nos. 3301 and 3315 (both 14 days old) were led to the feeder 3 m from the hive. Both performed *Sh* (*shaking*).

Following this warm-up (about 3 hours), 3 foragers were observed in June. No.184 performed only Sh (shaking) and TD (tremble dancing), and Hotaru and Blue showed strong persistence at the feeder without shrinking from twilight or severe rain.

(1) Shaking and tremble dancing by No.184

A 15-day-old forager, No.184, was observed on June 17, 2001. Only *Sh* (*shaking*) and *TD* (*tremble dancing*) were observed during 9 trips to the feeder within 1 m from the hive entrance and 3 excursions from the hive during 12:40 to 16:45 (Table 3) by only one observer. No.184 often departed for other unknown places and did not visit the feeder at 3 m in the last 3 flights. The next day, No.184 never visited the feeder but took off to other places.

(2) Loss of memory by Hotaru (an unknownaged worker)

An unknown-aged forager visited the feeder several times on June 18, 2001. One of the 3 observers marked it with white paint. The tip of its metasoma was painted so that its white tip resembled a firefly shining. Hence, we named it "Hotaru" (= firefly). When it visited the A-feeder several times, we decided to observe it continuously.

The dance performance of Hotaru is shown in Table 4. Sh (shaking), Da^r (round dancing) and Dat (transition dancing) were frequently observed during 65 trips. Only one TD (tremble dancing) was observed in the 11th trip. Though Hotaru visited the H-feeder at 15 m 20 times (25^{th} - 46^{th} trips), she did not perform Da^{*} (waggle dancing). We expected a reappearance of the waggle dance from 1978, Sapporo (Ohtani, 2000). As our expectation was not met, however, we moved the feeder farther from the hive. When Hotaru found the V-feeder at 65 m, it had become twilight. None of the other foragers were working at the entrance or the feeder. Da^{t4} (transition dancing with over 4 tail-waggings) was observed in the last 8 trips.

There was no observer available for the following 2 days. The feeding station was not open until 13:03 on June 21, 2001. The memory of the V-feeder (65 m) seemed to have disappeared from the brain of Hotaru. She did not visit the V-feeder on the 1^{st} trip, nor did she visit there after being forcibly transported to it (Table 5). We were obliged to move the feeder as close as 20 m from the

Table 3. Dance performances of a forager (No.184, 15 days old) visiting the A - C points of the movable feeder in the Gene Farm of the Museum of Nature and Human Activities, Hyogo. All behaviors were observed in the observation hive within the Mesh House on June 17, 2001 (slightly cloudy, 28.4 °C at 13:00). There are observed cases (\bigcirc) and non-observed cases (\times or a blank).

BEHAVIOR	shaking ¹⁾	tremble dancig ²⁾	round dancing		transition	dancing	3)	waggle dancing	FEEI	DING	UNKOWN
CODE	Sh	$Td' \leftarrow TD \rightarrow Td^{w}$	Da'	Da ^{t0}	Da ^{tl}	Da ^{t2}	Da ¹³	Da ^w	PL/	ACE	PLACE(S)
TRIP	The second	+ Eact	Ø	\bigcirc	\bigcirc	\bigotimes	\bigcirc	\bigcirc	DISTA FROM	ANCE HIVE (m)	FLYING OUT 1:firstly; 2:secondly; 3:thirdly
1 ⁴⁾ 2		Ø	××	× ×	× ×	× ×	× ×	× ×	A A	0.5 0.5	1
3	Ø	Ø	×	×	×	×	×	×	A	0.5	×
4	Ø	Ø	×	×	××	××	× ×	X X	A B	0.5 1	
6		Ø	×	×	×	×	×	×	В	i	x
7	Ø		×	×	×	×	×	×	В	1	2
8		0 0 0	××	×	××	××	× ×	× ×	B	1	2
9 10		0 0	×	x	×	×	×		B × ⁵⁾	3	1, 3 1
11			×	x	×	x	x	×	x	3	1
12 ⁶⁾			X	×	×	×	×	×	×	3	1

¹⁾ Seeley (1995) preferred 'shaking signal', and Schneider et al. (1998) used 'vibration signal'. The woodcut of *shaking* is copied from Hammann (1957). ²⁾ Seeley (1992) used 'tremble dance'. The woodcut is a part of the figure by Seeley (1992).

³⁾ Von Frisch (1967) divided Da^{\prime} into 4 sub-types as 4 woodcuts shown below. The woodcuts of Da^{\prime} and $Da^{\prime\prime}$ also from von Frisch (1967).

Volt Tisch ($\frac{1}{20}$) divided Da and r sub-types as 4 woodcuts shown below. The woodcuts of Da and Da also from von Frisch ($\frac{1}{20}$)

⁴⁾ The start time was 12:40. ⁵⁾ The \times -mark means that the bee could not visit the goal point.

⁶⁾ The observation was left off at 16:45.

entrance. Hotaru reached it after 50 s from departure and returned the hive after the 40-s-flight. To help her, we transported her to the point of 15 m, where Hotaru then flew out. Our "service" seemed to confuse Hotaru even more. Thereafter, she did not reach the K-feeder of 20 m continuously 4 times. Though she could reach the L-feeder of 25 m since the 13^{th} trip, she performed only *Sh* and *TD*.

(3) Waggle dancing by Blue (an unknown-aged worker)

After abandoning our study of Hotaru's behavior, we selected one of the foragers who had made several trips to the F-feeder at 7 m, but had no numbered disks. We marked it with blue paint and named it "Blue" on June 22, 2001. We moved the feeder farther after each time Blue visited the feeder twice at the same distance (Table 6).

Table 4. Dance performance of a worker, Hotaru (unkown age) visited the movable feeder at 0.5 to 65 m on June 18, 2001 (slightly cloudy, 26.4 °C at 11:00). There are observed cases (● or ◎) and non-observed cases (× or a blank). Dashed columns sygnify no observation.

BEHAVIOR	shaking	tremble dancig	round dancing		tran	nsition dai	ncing		waggle dancing	FLIGH	T TIME	FEED	DING
CODE	Sh	Td' ← TD → Td*	Da'	Da ¹⁰	Da' ¹	Da ¹²	Da ¹³	Da ¹⁴	Da ^w			PL/	
		Carly .	A		$\wedge \wedge$	$\wedge \wedge$	$\wedge \wedge$	(35)	m	HIVE	FEEDER	DISTA	
TRIP	M	+ 7	\bigcirc	$ \mathcal{W} $	\cup	\mathbb{C}	U		$ \cup $	FEEDER		POINT	(m)
01)	_	_		_		_			_			A	1
1 ²⁾		—	—		_	_	—	—			_	A	1
2		—										×	1
11	0	0	x x	××	×	×	××	××	× ×	5	5	A B	1 2
13			•							25	10	В	2 3
14 15			×	×	×	×	×	×	×	10 15	5 5	C C	3
16 17	Ø		××	××	× ×	× ×	× ×	×	× ×	35 5	10 5	D	4
18			×	x	×	×	x	x	×	30	5	D	4
19	©		×	×	×	×	×	×	×	20	5	E	5
20 21	Ø		×	×	×	×	×	×	×	10 25	10 5	E F	5 7
22										30	5	F	7
23 24			•							55 15	5 10	G G	10 10
25							~	v		120	5	Н	15 15
26 27			×	×	×	×	×	×	×	50 25	5 5	H H	15
28	0		×	X X	××	× ×	× ×	× ×	××	25 20	5 5	H H	15 15
<u>29</u> 30			×	×	Â	^	^	x	×		I 10	×	15
31	0		×	×	×	×	×	×	×	25	5	H .	15
32	Ø		×	×	×	×	×	×	×	10 10	5 5	H H	15 15
34 35					•					30 15	10 5	H H	15 15
36	0		•							10	10	H H	15
37			×	×	×	×	×	×	×	10 55	5 5	H H	15 15
39	Ø		Õ							10	5	н	15
40	0		×	×	×	. ×	×	×	×	20	10	н	15
41 42	Ô									10 10	10 5	H H	15 15
43 44							•			25 40	5 5	H H	15 15
45			×	×	×	×	×	×	×	1:	20	×	15
46	0		×	×	×	×	×	×	×	45	5 25	H X	15 20
48	Ű			•	•					20	10	I	17
49	<u> </u>									20	5	I J	17 19
50 51	Ø					•				5 20	5 10	K	21
52 53	Ø		×	×	¥	×	×	×	×	25 20	5 25	LM	23 25
54				Î	ě	^	^	^		40	10	M	25
55 56	6									25, 45 25	10 15	N P	30 35
57	0						ĕ			25	5	Q	40
58 59										25 35	15 10	R S	45 50
60			•					-				×	60
61			×	×	×	×	×	×	×	10	05	×	55
62 63				•				ĕ		20 35	35 15	T U	55 60
64 65 ³⁾	0		×	××	× ×	× ×	× ×	× ×	××	25	10	V ×	65 65
65"	U U		<u>^</u>	L ^	×	~	~	~	^	²	5		00

• $Da^{\prime 4}$ was the vigorous type of $Da^{\prime 3}$ in Ohtani (2002). See Table 1.

¹⁾ Hotaru was marked with white paint at 10:36 when she probably visited to A-feeder several times.
 ²⁾ The recording was started at 13:15. ³⁾ The trip finished at 19:18.

BEHAVIOR	shaking	tremble dancig	round dancing	_	tran	sition dar	ncing		waggle dancing	FLIGH	т тіме	FEED	DING
CODE	Sh	$Td' \leftarrow TD \rightarrow Td^{\vee}$	Da'	Da ^{t0}	Da 'l	Da ¹²	Da ¹³	Da ¹⁴	Da "			PLA	CE
TRIP	MAR .	+ Fold	0	\bigcirc	(χ)	(χ)	\bigcirc		\bigcirc	HIVE ↓ FEEDER	FEEDER ↓ HIVE	DISTA FROM	
01)	0		×	×	×	×		×	×	FEEDER		×	65
1 ²⁾	۲		×	×	x	x	x	x	×	2	15	×	65
2 ³⁾	Ø		×	×	×	×	×	×	×	1	5	×	65
3	O	0 0	×	×	×	×	×	×	×	50	40	к	20
4 ⁴⁾	Ø		×	×	×	×	×	×	×		85	к	20
5	0		×	×	×	×	×	×	×	3	70	×	20
6	Ø	Ø	×	×	×	×	×	×	×		0	×	20
7	0		×	×	×	×	×	×	×		35	×	20
8	Ø	0	X X	××	××	× ×	× ×	××	××	15	25 5	K K	20 20
10	Ő	0 0	×	Â	Â	x	x	x	x	15	5	K	20
11	0	©	×	×	·····×	····×	×	x	×		5	 К	20
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13	O	_	×	×	×	×	×	×	×	40	25	L	25
14	Ø	©	×	×	×	×	×	×	×	25	10	L	25
15	Ø		×	×	×	×	×	×	×	35	10		25
16 ⁵⁾	0		×	×	×	×	×	×	×	30	25	L	25

Table 5. Shaking and tremble dancing of Hotaru (unknown age) visiting the movable feeder at points 65, 20 and 25 m distant on June 21, 2001 (slightly cloudy, 23.5 °C at 13:10).

¹⁾ Shaking was observed several times till the first trip. The feeding station was opened at 13:03.

²⁾ The first trip was begun at 13:14.

³⁾ Hotaru was forcibly transported when she was suckking diluted honey on the small comb, and flew out from the point of 15 m.

⁴⁾ Hotaru was forcibly transported at 14:33:45 on the point at 20 m.

⁵⁾ The last trip was finished at 18:19:35.

BEHAVIOR	shaking	tremble dancig	round dancing			sition dar	ncing		waggle dancing	FLIGH	T TIME	FEED	DING
CODE	Sh	Td' ← TD → Td	" Da'	Da ¹⁰	Da "	D a ¹²	Da ¹³	Da ¹⁴	Da "			PL4	ACE
TRIP	YR)	+ Fact	6	\bigcirc	(χ)	(χ)	\bigcirc		\bigcirc	HIVE ↓ FEEDER	FEEDER ↓ HIVE	DISTA FROM	
	., (\vdash	00					FEEDER		F	7
0 ¹⁾		-	-		_			_	—				·
1 ²⁾	Ø	Ø	×	×	×	×	×	×	×	—		F	7
2	O	Ø	×	×	×	×	×	×	×	300	5	F	7
3	Ø	0 0	×	×	×	×	×	×	×	135	20	G	10
4	0 0	0	×	×	×	×	×	×	×	75	10	G	10
5	O	0	×	×	×	×	×	×	×	10	5	н	13
6	Ø	0	×	×	×	×	×	×	×	205	10	н	13
7		0 0	×	×	×	×	×	×	×	175	10	1	16
8		0	×	×	×	×	×	×	×	225	5	1	16
9	O	0 0	×	×	×	×	×	×	×	40	5	J	20
10	Ø	0		1						10	10	J	20
11	Õ	l õ			ĕ					60	5	м	25
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			×	^	^	^	^	^	│ ^ │	135	5	Q	40
19 ⁵⁾												Q	40

Table 6. Dance performance of a worker, Blue (unknown age) visiting the movable feeder at 7 to 40 m on June 22, 2001 (cloudy, 24.4 °C at 13:00). There are observed cases (\bigcirc or \bigcirc) and non-observed cases (\times or a blank). Dashed columns sygnify no observation.

¹⁾ Blue was one of workers which made several trips to the feeder, and was marked with blue paint.

 $^{2)}$ The recording was started at 14:06:30 when Blue returned hive.

³⁾ It means that Blue could not land the feeder. ⁴⁾ Blue tried again, but could not find the feeder.

⁵⁾ The observation was finished when Blue hesitated to go out at the entrance because of the gathering dusk,

but Blue had landed on the Q-feeder when it was put back at 19:24:40.

BEHAVIOR	shaking	tremble dancig	round dancing		tran	sition dar	ncing		waggle dancing	FLIGH	T TIME	FEE	DING
CODE	Sh	$Td' \leftarrow TD \rightarrow Td^{w}$	Da'	Da ^{t0}	Da 'l	Da ^{t2}	Da ¹³	Da ¹⁴	Da "			PL/	CE
TRIP	THE	+ EEC+	\bigcirc	\bigcirc	\odot	\bigotimes	\bigcirc		\bigcirc	HIVE ↓ FEEDER	FEEDER ↓ HIVE	DIST/ FROM	
0 ¹⁾	0			_						_		Q	40
1 ²⁾	Ŭ		×	×	×	×	×	×	×	1:	20	×	40
2 ³⁾			•							_	10	Q	40
3			×	×	×	×	×	×	×	25	10	Q	40
4	Ø		×	×	×	×	×	×	×	20	10	Q	40
5					•					10	5	Q	40
6										10	5	Q	40
7 8 ⁴⁾			×	× ×	××	× ×	××	××	××	60 20	10	R R	45 45
9 ⁵⁾		_	<u>^</u>		<u>^</u>	_	<u>^</u>	Â	Â	20		R	45
10 ⁵⁾												R	45
11 ⁵⁾		_										R	45
12										10	10	S	50
13						•	ĕ			25	10	S	50
14										65	10	S	50
15										50	10	S	50
16							-	•		35	10	Т	55
17							•	•		20	10	U	60
18			×	×	×	×	×	×	×		5	V	65
19			×	×	×	×	×	×	×	15	10	V	65
20							•	•		25	30	V	65
21 22			~		~	~				80	10	W	70
22			×	×	×	×	×	×	×	45 35	10 10	W Y	70 75
23		· · · · ·	×	×	×	×	×	×	×		5	Y	75
25						•		•		45	10	Ŷ	75
26	Ø		×	×	×	×	×	×	×	25	10	Ζ	80
27						•				35	10	ZA	85
28			×	×	×	×	×	×	×	240	15	ZA	85
29					•			•		230	10	ZA	85
30						•		۲		35	10	ZB	90
31	Ø					•				55	15	ZB	90
32						~		~		30	10	ZC	95
33 ⁶⁾			×	×	×	×	×	×	×	55	10	ZC	95

Table 7. Dance performance in rainy weather of Blue (unknown age) visiting the movable feeder at 40 to 95 m on June 23, 2001 (rainy, 22.1 °C at 13:10).

¹⁾ The observation was begun at 13:10.

²⁾ Blue flew out at 13:29:20, but could not find the Q-feeder.

³⁾ Blue on the small comb with diluted honey was forcibly transported the Q-feeder.

⁴⁾ The rain became severe from 5th trip, and Blue was saved and transported the hive becase she could not fly after getting soaked with rain.

⁵⁾ The observer at the hive was absent for another work.

⁶⁾ The last trip was finished at 17:45:35. It continued to rain strongly or weakly during the all trips.

Transition dancing with 1 or 1.5 tail-waggings (Dat1) was observed after the 10th trip; from the 10th to 14th trip, **Sh** (shaking) and **TD** (tremble dancing) were also observed (Table 6) and were probably indicative of unstable flight. Only **Da**^{t3} was observed on the 17th trip. However, Tdw (tremble walking) was again observed on the 18th trip. As twilight approached, Blue hesitated to go out from the entrance. We were going to close our observation, but found Blue feeding on the Q-feeder at 40 m.

The next day (June 23, 2001), the Q-feeder was opened at 13:10 because of rain during the morning. Blue flew out but did not reach the Q-feeder. Upon being transported to the Q-feeder, Blue returned to the hive and performed **Da**^r (round dancing) (Table 7).

It began to rain on the 4th trip, and the rain became severe from the 5th trip on, but Blue did not stop foraging. At last, Blue could not fly because of being soaked through. We saved her and transported her back to the hive. As soon as she was dry and warmed inside the hive, Blue began to visit the R-feeder. None of the other foragers worked in the field. Because the rain had become light, we moved the feeder farther from the hive. Da^{t4} (*transition dancing with over 4 tail-waggings*) were observed after visits to the S-feeder at 50 m. The feeder was moved to 95 m, but Blue still did not perform Da^w .

Table 8. The replacement by Blue (unknown age) of Daw by Dat4 as the feeder was moved (from 95 to 10 m) toward the hive on June 24, 2001 (fine after cloudy, 24.8 °C at 10:00).

BEHAVIOR	shaking	tremble dancig	round dancing		tran	sition dai	ncing		waggle dancing	FLIGH	T TIME	FEED	DING
CODE	Sh	$Td' \leftarrow TD \rightarrow Td^*$	Da'	Da "	Da"	Da ¹²	Da ¹³	Da "	Da"	HIVE	FEEDER	PLA	
	源	+ 35004	\bigcirc	\cap	()	(\mathcal{N})	(\mathcal{N})		(1)	L L	↓	FROM	HIVE
TRIP 0"	0 0			00	00		-		~	FEEDER	HIVE	POINT	(m) 95
1 ²⁾	0	_	×	×	×	×	×	×	×		-	zc	95
2 3	Ø		×	×	×	×	×	×	×	45	10 15	ZC ZC	95 95
4 5	Ø							•		40 20	10 10	ZC ZC	95 95
6 7									:	15 20	10 10	ZC ZC	95 95
8			×	×	×	×	×	×	×	20 20	15 15	ZC ZC	95 95
10									•	25	10	ZC ZC	95 95
11 12										20 15	10 15	zc	95 95 95
13 14									•	25 20	15 15	ZC ZC	95
15 16			×	×	×	×	×	×	×	25 10	10 10	ZC ZC	95 95
17 18										25 30	10 60	ZC ZC	95 95
19 20									•	50 40	15 10	ZB ZB	90 90
21 22										15 15	10 15	ZA Z	85 80
23										50	15	Z	80 75
24 25										20 20	10 15	Y	75
26 27										35 40	10 10	w	70 70
28 29										20 25	10 10	v v	65 65
30 31								٠	•	35 25	20 15	U U	60 60
32 33										25 30	15	T T	55 55
34 35			×	×	×	×	×	×	×	10 15	10 10	s s	50 50
36								÷		15	10	R	45 45
37 38										20 15	15 10	Q	40
39 40								•	•	25 20	15 10	Q Q	40 40
41 42										40 20	20 10	P P	35 35
43 44										20 20	10 10	0	30 30
45 46			×	×	×	×	×	×	×	95	20	N N	25 25
47 48								ě		40	5	M	20 20
49								•		15	5	L	15
50 51 ³⁾	_	_	_	-		_	_	•	—	15 65	5 5	K	15 10
52 53	_	-		=		_	_			_	5	K K	10 10
54 55			_	-	_	_	_	•	_	20 15	10	K K	10 10
56 57	-	-		-	_	_	_	٠	-	15	10	к К	10 10
58 59								•		10 55	5 10	к к	10 10
60 61			×	×	×	×	×	×	×	80 35	10 5	к к	10 10
62 63	—	-	-	-	_	—	_	-	-	10	5	ĸ	10 10
64 65					_	_	_	i		 10	10 5	ĸ	10 10
66			×	×	×	×	×	×	×	10	20	к	10
67 ⁴⁾ 68			× ×	× ×	× ×	×	× ×	× ×	× ×	10 15	280 5	K K	10 10
69 70					•					15 30	10 10	к К	10 10
71 72			×	×	×	×	×	×	×	50 40	10 10	к к	10 10
73 74			×	×	×	ê	×	×	×	25 20	5	ĸ	10 10
75		. 0	×	×	××	×	××	××	×	15	5	ĸ	10 10
76 77 ⁵⁾		U	×	×		×			×	20 20	5 5	к	10
78 79			× ×	× ×	× ×	× ×	× ×	× ×	× ×	40 30	5 5	к к	10 10
80 81 ⁵⁾			×	×	×	×	×	×	×	15 15	5 5	K K	10 10
82				×	×	×	×	×	×	40	5	ĸĸ	10
83 84			× × ×	× ×	× ×	× ×	× ×	× ×	× ×	20 20	5 5 5	К	10 10
85 ⁵⁾ 86			×	×	×	×	×	×	×	15 50	5 5	К К	10 10
87 88			× ×	× ×	× ×	× ×	× ×	× ×	× ×	25 35	5 20	K L	10 15
89 90	0		× ×	× ×	×	× ×	×	× ×	× ×	15 15	5 35	L	15 15
91 92	4		×	××	×	××	××	××	××	40	5 5	L	15 15 15
93 ⁶⁾			×	×	× ×	×	×	×	× ×	45 35	5 5	L	15
)		egun at 10:00.											

¹⁾ The observation was begun at 10.00.
²⁾ Blue on the small comb with diluted honey was forcibly transported the ZC-feeder at 10.48.

⁶ Blue lottered long time of the way hive for the unknown cause.
 ⁹ Dat (round dancing) were observed once or uncompletely.
 ⁹ The last trip was finished at 18.21.20.

The next day (June 24, 2001), the feeding station (ZC-95 m) was open at 10:00 (Table 8). Blue did not go out easily. Losing our patience, we forcibly transported Blue to the ZC-feeder. Blue soon began to perform Da^t (transition dancing), and finally performed Da^w (waggle dancing) on the 6th trip. It was the 3rd time that the waggle dance of a particular individual had been observed since the first observation in 1978 (Ohtani, 2000). This was our chance to observe where Da^w was replaced

with Da' in the trial as the feeder was moved nearer to the hive. We had to double-check the description by von Frisch (1967): "From about 25 to 100 m is the region of transition from round dance to tail-wagging dance", which is probably inexperienced to almost all researchers on dance performances.

After the confirmation of Da^{*} (waggle dancing) in 13 successive trips, we tried to move the feeder nearer to the hive (Table 8). Blue continued to

		r –							1	I			
BEHAVIOR	shaking	tremble dancig	round dancing			sition dai			waggle dancing	FLIGH		FEED	
CODE	Sh	$Td' \leftarrow TD \rightarrow Td^{w}$	Da'	Da ^{t0}	Da'l	Da 12	Da	Da ^{ti}	Daw			PL4	
	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	met t			$\sim \sim$	$\wedge \wedge$	$\wedge \wedge$	02	m	HIVE	FEEDER	DISTA	
	TAR:	A CHO	( ()	(X)	$(\chi)$	$(\chi)$	$(\gamma)$	$\left(\begin{array}{c} \frac{1}{2} \\ \frac{1}{2} \end{array}\right)$			↓ 		
TRIP	77.5			$\overline{\bigcirc}$	00	00	$\underline{\cdots}$			FEEDER	HIVE	POINT	(m)
0 ¹⁾	Ø		-					_	-			A	1
1 ²⁾			×	×	×	×	×	×	×	5	5	A	1
2			×	×	×	×	×	×	×	5	5	A	1
3										5 185	10 40	A B	1 2
5			-							70	5	B	2
6 ³⁾										220	10	×	3
					ĕ					50	20	c	3
8					ĕ					40	30	c	3
9										20	10	D	4
10										60	40	D	4
11 ⁴⁾	—	_			—			_	—	5	5	D	4
1 ⁵⁾											15	с	3
2					•					30	10	C C	3
3							ĕ			50	25	l č	3
4								•		80	10	C C	3
5							•			140	10	D	4
6										85	10	D	4
7										95 80	15 25	E	5 5
9			×	×	×	×	×	×	×	70	10	E	5
10			×	×	×	×	×	×	×	55	10	E	5
11			×	×	×	×	×	×	×	15	15	E	5
12			×	×	×	×	×	×	×	50	10	Е	5
13										10	40	F	6
14						•				25 20	35	G G	7
16			•				•			20	10	Ĥ	8
17			×	×	×	×	×	×	×	50	_	н	8
18			×	×	×	×	×	×	×	25	10	I	10
19										15	15	I	10
20						•	-			25	15	J	12
21												J	12
22 23			×	× _	×	×	×	×	×	20		к к	15 15
23			_			•				15	10	L	18
25			×	×	×	×	×	×	×	25	10	L	18
26							•				35	м	21
27 ⁶⁾							•				25	м	21

**Table 9.** Dance performance of B883 (16-17 days old) visiting the movable feeder at 1 to 4 m on August 16 (fine & cloudy, 35.3 °C at 10:40), and from 3 to 21 m on August 17, 2001 (fine & cloudy, 31.3 °C at 11:10).

¹⁾ B883 performed *shaking* after she was transported forcibly to the A-feeder at 09:57, 10:59 and 11:12.

²⁾ B883 visited the A-feeder at 11:26. **Da^{t1}* was performed horizontally on the passage to the entrance.

³⁾B883 could not reach the C-feeder, but landed the vicinity and rested there for 65 s.

⁴⁾ The observation was finished at 12:33 soon after B883 returned hive, because of the urgent other work of the observers.

The observation was resumed at 17:00, but B883 did not visit the D-feeder till 19:00.

⁵⁾ The observation was begun at 08:00, but B883 did not visit the A-C feeder till 10:58 in spite of the visit of other visitors.

⁶⁾ B883 entered the hive at 14:08:00, which was the last trip. No visitor was observed in the N (25 m)-feeder during 14:25 - 17:00.

perform  $Da^{*}$  with the V-feeder at 65 m, but performed  $Da^{*}$  and  $Da^{t4}$  when the feeder was from 60 m to 40 m, and did not perform  $Da^{*}$  when the feeder was closer than 40 m from the hive. During 55 to 64 visits, Blue always performed  $Da^{t4}$  never  $Da^{*}$  with the K-feeder at 10 m. Table 8 finds that the distance of 60 m was required for steady  $Da^{*}$ , at least for Blue.

#### 3. B883 in the August observation

The next individual marking started on July 4, 2001. The feeding station was opened at 15:26 on August 15, but the feeder at 2 m was closed at 18:20 because of a thunderstorm. There were 3 regular visitors (B835, B883 & B895).

The next day (August 16), the A-feeder at 1 m was opened at 9:30, and B883 (16 days old) was

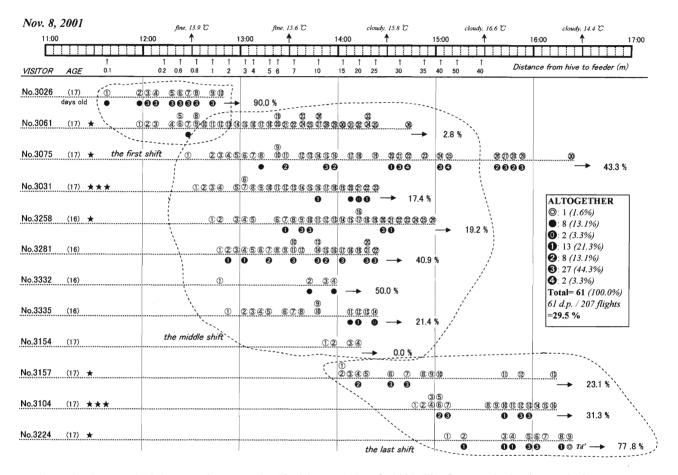
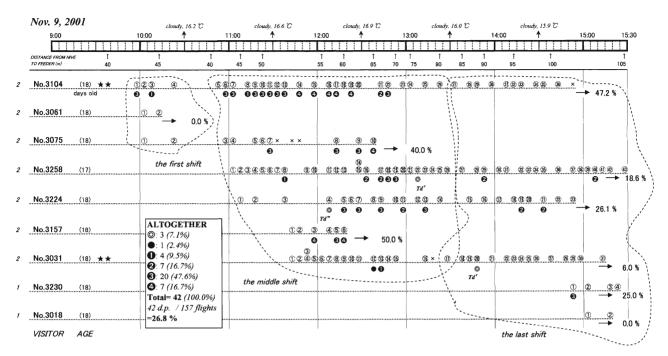


Figure 3. The record of dance performances by 12 visitors on Nov. 8, 2001. The first row is the time scale from start to end of our observation, with weather and air temperature (upper side), and distance from hive to feeder (under side). The numbers in the white circles denote the trip number. Double circles denote the performance of TD (tremble dancing,  $Td^r$  or  $Td^w$ ). Black circles denote various dance performances: circled numbers correspond to transition dancing from  $Da^{t0}$  to  $Da^{t4}$ ; empty black circles indicate round dancing. All foragers performed various dances at various rates (the dance appearance rate = the number of dance performances / the number of flights); these rates are shown after the arrows. A star indicates that the individual appears again in following figures. Three shift groups seemed to forage alternately (see, 3 broken-line borders).

transported to the A-feeder 3 times (9:56, 10:59 & 11:12). B883 at last began to visit the A-feeder at 11:26. She visited the D-feeder at 4 m on the 11th trip, and performed  $Da^{t3}$  (Table 9, the upper part). We twice observed  $Da^{t1}$ , performed horizontally on the passage to the hive entrance. Because of other, more urgent work, we interrupted our observation from 12:33 to 17:00. The D-feeder was

again opened at 17:00, but B883 had not visited the feeder by 19:00, when the feeding station was closed.

The next day (August 17), the C-feeder at 4 m was opened at 8:00. It was 10:58 when B883 finally visited this feeder. B883 performed  $Da^r$  or  $Da^{t1-t4}$  in her 27 trips, but did not fly after her last flight at 14:08 (Table 9, the lower part). The others' foraging of the hive was inactive for some unknown reason.



**Figure 4.** The record of dance performances by 9 visitors on Nov. 9, 2001. The basic explanation is the same as in Figure 3. The distance of the feeder was 40-105 m from the hive. The head number of each individual denotes the number of days visiting. New visitors have the number "1", of course. There are 3 shift groups: the first, middle and last shift.

#### 4. Many foragers in the November observation

The last marking in 2001 was carried out for 4 days on October 23-26. The total number of marked bees was 770 (=238+141+236+155). All of the bees had been marked with numbered disks. Forcible transportation was attempted on November 6-7, but no regular visitors were observed. On Nov. 8, 12 regular visitors were observed in the movable feeding station from 0.1 m to 40 m. On Nov. 9, 9 foragers regularly visited the feeder from 40 m to 105 m. On Nov. 10, no visitor was observed because of a strong wind (wind scale, 3 or 4; 17.2 °C). Four visitors on Nov. 11 and 7 visitors on Nov. 12 were observed at the feeder over 100 m distant. After no observation for 2 days (Nov. 13-14), the only regular visitors were No.3104 on Nov. 15 and No.3158 on Nov. 16-22.

## (1) Twelve regular visitors on Nov. 8 (feeder: 0.1-40 m)

Several regular visitors began to appear after No.3026 visited the feeder of 0.1 m at 11:44:55 (Figure 3). The most crowded the feeder got was with 8 visitors out of the 12 regular foragers, who showed various dance performances. The dance appearance rate (=the number of dance performances / the number of flights) was calculated for each individual. Rates of over 50 % were observed in 3 foragers (Nos. 3026, 3332 & 3224). On the other hand, rates under 20 % were observed in 4 others (Nos. 3061, 3031, 3258 & 3154). The dance appearance rate in crowded conditions with many visitors is considerably lower than that when only a single visitor is feeding (cf. all tables, discussed later). None of visitors performed  $Da^{*}$  (waggle dancing) after visiting the feeder at 0.1-40 m.

There seemed to be 3 alternate foraging shifts at the movable feeder: the first shift, the middle one and the last one (see broken-line borders in Figure 3). It is unclear whether these shifts were influenced more by the foragers' territories or their activity times.

# (2) Nine regular visitors on Nov. 9 (feeder: 40-105 m)

The next day (Nov. 9), the feeding station at 40 m was opened at 9:00. Continuous regular visitors included 7 foragers from the previous day and 2 new visitors appearing before and after 15:00, respectively (Figure 4). Their dance performances were various in terms of patterns of appearance; however, the appearance rates of  $Da^r$ ,  $Da^{t0}$  and  $Da^{t1}$  dropped and the rate of  $Da^{t4}$  rose compared to those of the previous day (Figure 3: cf. ALTOGETHER boxed). Though the distance from hive entrance was over 100 m, no  $Da^w$  was

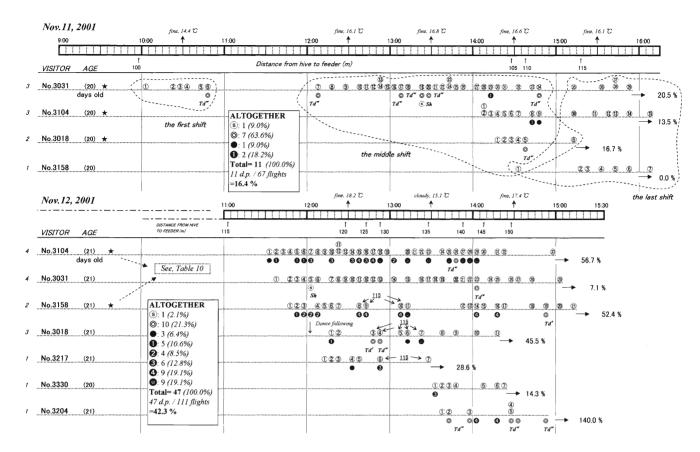


Figure 5. The records of dance performances by 4 visitors on Nov. 11, and 7 visitors on Nov. 12, 2001. The basic explanation is the same as in Figures 3 and 4. The letter 's' in a circle denotes Sh (shaking). The white letter 'w' in a black circle means  $Da^{w}$  (waggle dancing). The distance of the feeder was 100-150 m from the hive. Though 3 shift groups can be faintly perceived in the upper part, they were scarcely apparent in the lower part of this figure. The feeder was movable, but the small comb with the diluted honey was left at a point 115 m away; Nos. 3158, 3018 and 3217 stopped on their way to the feeder at 120-135 m (see, '115' with arrows in this figure).

observed. Again, there seemed to be 3 shifts (see broken-line borders in Figure 4).

### (3) Four and 7 regular visitors on Nov. 11-12 (feeder: 100-150 m)

The next day (Nov. 10), bad weather (primarily the strong wind) prevented the regular foragers from visiting the feeder at 105 m. This interruption seemed to discourage visitors on Nov. 11 (Figure 5).  $Da^{t2}$ ,  $Da^{t3}$  and  $Da^{t4}$  disappeared, Shappeared and TD increased, as shown in the upper part of Figure 5. The appearance rate of dance performances was the lowest of the November observations (16.4 %, cf. ALTOGETHER). The three shifts were less distinct: No.3032 was an

Table 10.	The fe	eeder	(150-	155 m	from	the	hive)	visited	by	the $2$	worker	s
(No.3104	or No.31	158)	on Nov	ember	15-18,	200	1.					
DATE	IND. NO.	AGE	DISTANCE OF	OPENING	OF TF		SIT TIME	NI DURATIO	N (s)	TEMP.(°C)	Da	1

DATE	IND. NO.	AGE	DISTANCE OF FEEDER (m)	OPENING OF FEEDER	TRIP	VISIT TIME	NI DURATION (s)	TEMP.(°C)	Da OBSERVATION
Nov. 15, 2001	3104	24	150	15:00~15:55	1	15:26:00	375	12.7	_
			150		2	15:36:00	210	11.5	
			150		3	15:49:00	300	11.6	
Nov. 16, 2001	3158	25	150	15:00~16:05	1	15:17:25	170	13.5	_
			150		2	15:24:20	95	12.9	_
			150		3	15:30:25	50+15	12.8	
			150		3 4 5 6 7	15:33:40	45	12.8	_
			150		5	15:39:15	45	12.7	_
			150		6	15:41:15	115	12.7	_
			150		1	15:47:35	225	12.5	
			150		8	15:57:15	15+85+15	12.4	—
Nov. 17, 2001	3158	26	150	13:55~16:00	1	14:30:50	215	13.8	non
			151		034567	14:38:10	90	13.7	non
			153		3	14:45:10	230	13.6	non
			153		4	14:54:00	225	13.6	non
		{	155		5	15:02:25	100+40+100	13.6	non
		5	155		6	15:13:00	110	13.8	non
			155			15:20:25	180	13.6	non
			155		8	15:27:25	265	13.4	Da ^w
			155		9	15:35:40	20+200+10+10	13.1	Daw
			155		10	15:47:15	300	12.8	Da "
Nov. 18, 2001	3158	27	155	14:02~15:02	1	14:04:55	250	12.0	non
			155		2	14:12:50	220	11.7	non
			155		3	14:23:45	145+20	11.7	non
			155		4	14:32:35	245	12.2	non
			155		5	14:44:10	170	10.6	non

all-rounder, No.3104 was in the middle + last shift, No.3018 was in the middle shift, and No.3158 was in the last shift. The movable feeder started at 100 m, but reached only 115 m.

The next day (Nov. 12), the 4 regular visitors were observed, and 3 of them performed  $Da^{w}$  (No.3104: 130 m; Nos.3018 & 3158: 115 m). Three new visitors were recruited, but none of them performed  $Da^{w}$ . There were 3 shifts unclearly perceived (all-rounders: Nos. 3104, 3031 & 3158;

middle shift: Nos. 3018, 3217 & 3330; last shift: No.3204). The distance of the feeder was extended to 150 m (the lower part of Figure 5).

There was an accident in the feeding station at 115 m on Nov. 12. The visitors were fed from a small comb on the feeder, but the small comb was accidentally dropped to the ground by a human observer. Another small comb was newly adopted on the feeder. The dropped comb was left on the ground when the feeder was moved to the point at

**Table 11.** Dance performance of a worker, 3158 (28-31 days old) visiting the fixed feeder at 155 m on November 19 - 22, 2001. There are observed cases ( $\bullet$  or  $\bigcirc$ ) and non-observed cases ( $\times$  or a blank). Dashed columns sygnify no observation.

$\begin{array}{c c c c c c c c c c c c c c c c c c c $												r			
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	BEHAVIOR	piping ¹⁾	shaking	tremble dancig	round dancing		tran	sition dar	ncing		waggle dancing	FLIGH	TTIME		
Image: Now. 19         Image: Now	CODE	Pi	Sh	$Td' \leftarrow TD \rightarrow Td^{w}$	Da'	Da ¹⁰	Da''	Da '2	Da	Da "	Da ^w			PLAC	CE
TRUE         PT         P	$\sim$		~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	met 1			$\sim \sim$	$\wedge \wedge$	00	<u></u>	m				
Nov. 19     fine, 1.3.8     C at 12:00     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x     x	TOID	W.K.	The second	1 70		(X)	(X)	$(\chi)$	$(\gamma)$	(\$)					
1 ⁷¹ Image: Big Stress St		Guo 12.8	97 - 12.00			00		~~~	~~~			FEEDER	HIVE	POINT	(m)
2       0       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x       x		<i>Jine</i> , 15.0	C al 12:00									- FO			155
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1) Ohtani & Kamada (1980) used 'worker piping', and Ohtani (1994) used 'piping (Pi)'. The woodcut of piping is copied from Ohtani & Kamada (1980).

 $^{2)}$  The feeder was opened at 11:00, and the first trip started at 11:10:20.

³⁾ The aged worker, No.3158, landed on the ground and rested for 55 s after flying for 40 s.

⁴⁾ The last trip finished at 13:53:30, and piping soon started within the hive.

⁵⁾ The first trip started at 11:07:20 after the stimulation by diluted honey at 11:03:00.

⁶⁾ The last trip finished about at 13:13, and *trembling dancing (Td")* started at about 20 min later.

⁷⁾ The feeder was opened during 14:20 to 15:40, and the only one trip was from 14:10:55 to 14:14:05. Honey intake on the feeder lasted for 25 s.

⁸⁾ The feeder was opened during 13:20 to 15:00, and the 1st trip was from 13:47:15 to 13:50:00. Honey intake on the feeder lasted for 55 s.

 $^{9)}$  The 2nd trip was from 14:23:00 to 14:55:05. Honey intake on the feeder lasted for 10 s.

BEHAVIOR	shaking	tremble dancig	round dancing	transition dancing				waggle dancing FLIGH		T TIME	FEEDING		
CODE	Sh	Td' ←TD →Td*	Da'	Da ' ⁰	Da' ¹	Da '2	Da ¹³	Da '4	Da "			PL/	ACE
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2			×	×	×	×	×	×	×	10	5	on	0.3
3			×	×	×	×	×	×	×	15	5	on	0.5
4			×	×	×	× .	×	×	×	20	5	on	0.5
5			×	×	××	×	× ×	××	X X	5 10	5 15	on	0.6
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10			×	×	×	×	×	×	×	15	5	on	2
11	Ø		×	×	×	×	×	×	×	5	5	on	2
12	0		×	×	×	×	×	×	×	50	5	on	3
13	Ø		×	×	×	×	×	×	×	-	5	on	3
14	Ø		×	×	×	×	×	×	×		5	on	4
15	0		×	×	×	×	×	×	×	5	5	on	4
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39			×	×	×	×	×	×	×			on	15
40 ⁴⁾								-			_	on	15

**Table 12.** Dance performance of Pink (probably 40-43 days old) visiting the movable feeder at 0.3 to 15 m on September 16, 2003 (fine, 26.2 °C at 11:00).

¹⁾ Pink, on the small comb with deleted honey, was forcibly transported to the feeder at 11:52.

²⁾ Pink visited the feeder at 0.3 m at 12:47.

³⁾ Pink went out in the Mesh House from the slit of the hive entrance. She was caught with an insect net, and released out of the Mesh House

⁴⁾ The last trip was finished at 17:27:20. The observation was broken off at 17:30:00 contrary to the bee's desire.

120 m. No.3158 did not reach the feeders at 120-135 m, after emerging from the entrance of the hive. However, No.3158 performed  $Da^{t4}$  and  $Da^{w}$  upon returning to the hive (the 8th - 11th trip, see 3rd row in the lower part of Figure 5). It was the dropped comb that No.3158 visited on her way to the feeding station at 120-135 m. Nos. 3018 and 3217 also were attracted to the stopover comb. The removal of the small comb seemed to cause a new confusion: No.3158 ceased to fly for over 30 min, No.3018 did not dance at all, and No.3217 did not fly out at all.

# (4) Behaviors of No.3104 on Nov. 8-15 (feeder: 30-150 m)

There were no observers on Nov. 13 and 14. The

feeder at 150 m was again opened at 15:00 on Nov. 15. After 26 min from the opening, only No.3104 visited the feeder. For our other works, the feeder was closed at 15:55. No.3104 could forage 3 times in the cold condition  $(11.5-12.7^{\circ}C)$ , but did not perform  $Da^{*}$  (Table 10).

No.3104 was a regular visitor since Nov. 8 (cf. Figures 3-5). Her rate of dance appearances changed as follows: <u>31.3</u> %, <u>47.2</u> %, 13.3 %, <u>56.7</u> % and 0.0 %. The numbers underlined were over the average. **Da**^w was observed only in the case of 56.7 %.

### (5) *Waggle dancing* and *piping* of No.3158 on Nov. 11-22 (feeder: 100-155 m)

No.3158 was first observed on Nov. 11 (cf. Figure 5). Her rate of dance appearances changed as

follows: 0.0 % (7 flights), 52.4 % (21 flights), 0.0 % (8 flights), 30.0 % (10 flights), 0.0 % (5 flights), 95.8 % (24 flights), 94.4 % (18 flights), 100 % (1 flight) and 100 % (2 flights). The first 2 cases are detailed in Figure 5, the next 3 cases in Table 10, and the last 4 cases in Table 11. Da^w (waggle dancing) was observed in the cases of 52.4 %, 30.0 %, 95.8 % and 94.4 %. In the last 2 cases, the rates of **Da**^w appearance were 75.0 % and 72.2 % (Table 11). Another special mention from Table 11 is that piping (Pi) was observed twice on Nov. 19. Though its vibration was as weak and the piping sound could not be heard, its style was one and the same as that Ohtani and Kamada (1980) observed: "Head raised, mesosoma pressed to the substratum, metasoma slightly raised, wings slightly spread and vibrated through their whole length."

# 5. One forager in the September observation in 2003.

Another trial in 2003 was carried out with the same trial set-up as in 2001. One queen and about 1,200 bees were introduced to the observation hive and the individual marking started on August 6. A total of 1,300 marked bees were released into the observation hive. The last 100 bees were marked on September 7. Over 90 % of the non-marked bees were replaced by marked bees (Nos.1-1299).

### (1) Piping of No.43 and a regular forager, Pink (probably 40-42 days old)

Forcible transportation started on September 14. No.199 (38 days old) performed  $Td^{w}$  when she returned from the feeder at 0.5 m, and No.43 (39 days old) performed *Sh* (*shaking*) and *Pi* (*piping*) once, but no regular visitors were observed.

At 11:28 on Sept. 15, 13 workers were forcibly transported to the feeder at 0.3 m. A non-marked forager visited the feeder at 11:59. No.266 (38 days old) visited the feeder at 13:35 and the non-marked forager returned at 13:40. The non-marked bee was marked with a pink marker and named "Pink". Her age was inferred to be 40-43 days old because she probably was a young worker (1-3 days old) when she was introduced into the observation hive on Aug. 6. Pink visited the 0.3-m-feeder again at 13:56 and 14:16. The distance of the feeder was extended to 0.6 m, but Pink did not visit it further.

On Sept. 16, the 0.3-m-feeeder opened at 11:00, and 6 workers were forcibly transported the feeder, but there were no regular visitors until 12:47. About that time, we observed that No.43 (40 days old) performed many pi at the observation hive. The piping sound could be heard clearly (cf. Ohtani & Kamada 1980).

Pink began to visit the 0.3-m-feeder from 12:47 on. She performed 15 Sh, 1  $Da^r$  and 17  $Da^t$  with the feeder at 1.5 to 15 m (Table 12). There was only one observer after the  $33^{rd}$  trip, and the observation was broken off at 17:30 for the observer's convenience.

### (2) No Da^w by Pink on the feeder of 155 m

On Sept. 17, Pink regularly visited the feeder at 15 to 155 m. The feeder at 15 m was opened at 10:00. The feeder was moved back each time after Pink visited it twice at the same distance from the hive. Pink performed only *Sh* until the 15th trip to the feeder, at 45 m. She performed  $Da^{t0}$  on the 22nd trip to the feeder, at 60 m, and  $Da^{t4}$  from the 25th trip to the feeder at 80 m, but no  $Da^{w}$  at the feeder at over 100 m (Table 13). Pink never performed  $Da^{w}$  after reaching the feeder at 155 m, though No.3158 performed  $Da^{w}$  after visiting the fixed feeder at 155 m in 2001 (cf. Table 11).

The next day (Sept. 18),  $Da^*$  by Pink was expected to be observed as a matter of course. The feeder at 155 m was opened at 10:00. There were no visitors. Pink was performing  $Td^*$  in the observation hive. Pink was stimulated with the diluted honey used at the feeder. She visited the feeder at 155 m once, but she performed  $Td^*$ continuously for about 2 hours. Thereafter, Pink went out to another place and returned with pollen. Stimulation by feeder honey was again tried. Pink flew out near the feeder, but did not land. This abrupt confusion was thought to be caused by senility.

#### Discussion

The intention of our trials was to locate some of the concealed problems in the experimental procedure by von Frisch. An indispensable regular procedure is to abbreviate details, and this is apt to prevent reporting on new or accidental facts. We reported our observations in great detail and exactly, but our discussions below might still be limited because our understanding of dance performances is still in its beginning stages.

# 1. Shaking or piping as an outlet of excitement in bee flights

Seeley (1992, 1995) speculated that Sh (shaking) is an awakening signal to rouse a troop of foragers. Ohtani (1994) speculated that shaking to a queen (wSh/q) might be a displacement behavior due to a state of conflict between 2 drives, fleeing and aggression. Ohtani (2002) also speculated that Sh could be a displacement behavior due to a state of conflict between 2 behaviors, dancing and resting, from the observation of Sh in the early morning and/or the evening. Such Sh was also observed in the present trial (Tables 7-9, 13).

Another property of **Sh** was its frequent occurrence (Tables 4-6, 12). The common situation for **Sh** is having the feeder closer than 40 m and simultaneous *transition dancing* with 3 or fewer tailwaggings ( $Da^{t\theta} \sim Da^{t3}$ ). Schneider et al. (1998) concluded that **Sh** (=vibration signal) plays a general excitatory role in the context of house hunting by

**Table 13.** Dance performance of Pink (probably 41-44 days old) visiting the movable feeder at 15 to 155 m on September 17, 2003 (fine, 27.7 °C at 10:00).

DEU MOD		the state of the state				aitian dan	aina			FUICH	T TIME	CCEL	DING
BEHAVIOR	shaking Sh	tremble dancig Td' ←TD → Td"	round dancing Da'	Da ¹⁰	Da ¹¹	sition dar. Da ¹²	Da ¹³	Da ''	waggle dancing Da ^w	FLIGH		PLA	
CODE	Sn		Da	Du	Du	Du	Du		Du	HIVE	FEEDER	DIST	
	X	+ 354	8	m	$\sim$	$\wedge$	$\bigcirc$				FEEDER ↓	FROM	
TRIP	MR.	¥ 0		$ \mathcal{M} $	$\mathcal{O}$	$\mathcal{O}$	U	V		FEEDER	+ HIVE	POINT	(m)
TRIP										FEEDER			
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2			×	×	×	×	×	×	×		10	on	15
3	Ø		×	×	×	×	×	×	×	10	10	on	17
4			×	×	×	×	×	×	×		10	on	17
5	Ø		×	×	×	×	×	×	×	25	5	on	20
6	Ø		×	×	×	×	×	×	×		5	on	20
7	Ø		×	×	×	×	×	×	×	40		on	25
8	Ø		×	×	×	×	×	×	×		15	on	25
9	Ø		×	×	×	×	×	×	×	-		on	30
10			×	×	×	×	×	×	×		15	on	30
11	O		×	×	×	×	×	×	×	20	5	on	35
12	O		×	×	×	×	×	×	×		5	on	35
13	O		×	×	×	×	×	×	×	30+	15	on	40
14			×	×	×	×	×	×	×	15		on	40
15	Ø		×	×	×	×	×	×	×	25 ²⁾	5	on	45
16	Ĩ		×	×	×	×	×	×	×	—	15	on	45
17			×	×	×	×	×	×	×	15	15	on	45
18	1		×	×	×	×	×	×	×	-	30	on	50
19			×	×	×	×	×	×	×	20		on	50
20			×	×	×	×	×	×	×			×	60
21			×	×	×	×	×	×	×	140	15	on	60
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33	~							•		50	20	on	105
34	Ø							•		25	10	on	105
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36										25	15	on	110
37								•		75	10	on	115
38								•		25	20	on	115
39								•			25	on	120
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41								•		40	20	on	125
42								•		15	25	on	125
43								•		20	25	on	130
44								•		—	30	on	130
45								•		40	25	on	135
46			×	×	×	×	×	×	×			on	135
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										25	25	on	
54										20	20	on	155 155
55							~		×			on	
56	6		×	×	×	×	×	×		110	30	on	155
57	Ø		×	×	×	×	×	×	×	110	35	on	155
58	6							•		30	25	on	155
59	O		×	×	×	×	×	×	×	25	20	on	155
60 ³⁾	Ø		×	×	×	×	×	×	×	100	20	on	155
L													

¹⁾ The feeder at 15 m was opened at 10:00.

²⁾ Pink went out in the Mesh House from the slit of the hive entrance. She was caught with an insect net, and released out of the Mesh House.

³⁾ The last trip was finished at 17:50:00. The observation was finished at 18:00:00.

swarming bees. Recently, Schneider and Lewis (2004) argued that Sh has the role of modulatory communication and the organization of labor. If Sh is a displacement behavior, it would be ordinary for Sh to appear in tense situations of crucial importance for the colony.

One metaphorical idea I had was that Sh may be "a starter motor" to start the dancing "engine". The awakening function by Seeley (1992) may apply to shaking the worker's self rather than other workers.

Ohtani and Kamada (1980) reported Pi (*piping*) by laying workers and guarding workers, and suggested it to be comparable to quacking and tooting, respectively, of queen piping. Pi could be a displacement behavior, as Fletcher (1978) suggested of queen piping. The Pi that we observed seemed to have similar conditions for appearance. The Pi in Table 11 seemed to be a substitute of Sh (shaking).

If  $Da^*$  (waggle dancing) is an imitation flight (ohtani, 2000) or a miniaturized re-enactment of dancer's recent journey (Seeley, 1995), *Sh* and *Pi* could be thought to be outlets of excitement from flight.

# 2. The condition for the appearance of *waggle* dancing

Reading through Schneider et al. (1998), Srinivasan et al. (2000), Esch et al. (2001) and Arnold et al. (2002),  $Da^{w}$  (waggle dancing) seems to be a stable behavior pattern. Nevertheless, Ohtani (2000, 2002) scarcely encountered  $Da^{w}$ . Also in this trial, we sometimes did not encounter  $Da^{w}$ , even when the feeder distance was over 50 m from the hive (cf. Tables 4, 5, 7 & 13; Figures 4 & 5 upper). It was with the feeder at 95 m that Blue performed  $Da^{w}$  on June 24 in 2001 (cf. Table 8), and it was

STUDY YEAR	VISITOR(S)	AGE DANCE PERFORMANCES		NO.TRIPS d.p. SEEN	NO. ALL TRIPS	APPE	APPEARANCE RATE		OBSERV- ATION DAY	REFERENCES	
1978	D6	unknown	Sh, Td ^w , Da', Da ^t , Da ^w	16	33	0.485		0.458	Oct. 3	Table 1	
1999	W1110	unknown	Da', Da'	4	14	0.286			Nov. 10	Table 2	
	Wp12	unknown	Sh, Td ^w , Da ^t	11	14	0.786		0.597 0.647	Nov. 14	Table 3	Ohtani (200
	Wb13	unknown	Sh, Td', Da', Da'	10	14	0.714			Nov. 24	Table 4	
	Wb13	unknown	Sh, Da', Da'	12	20	0.600	0.047		Nov. 25	Table 4	
	No.874 (No.862	13	Td', Td ^w , Da', Daʻ	5	18	0.278	- N.		Nov. 6	Table 3	
	No.862 (No.874	14	Da', Da ^t	15	28	0.536	0.612		Nov. 6	Table 4	
	No.874 (No.862	14	Sh, Td', Da', Da'	51	75	0.680	0.012		Nov. 7	Table 5	
	No.862 (No.874	15	Sh, Td', Da'	33	49	0.673			Nov. 7	Table 6	
	No.874	15	Td ^r , Td ^w	9	10	0.900			Nov. 8	Table 8	1
	No.874	16	Sh, Td', Td ^w	6	9	0.667			Nov. 9	Table 8	1
2000	No.874	17	Sh, Td ^r , Td ^w	15	15	1.000		0.766	Nov. 10	Table 8	Ohtani (200
	No.874	18	Td', Td ^w	7	7	1.000			Nov. 11	Table 9	1
	No.874	19	Sh, Td', Td" Da', Da'	27	27	1.000	0.919		Nov. 12	Table 9	1
	No.874	20	Da ^t	35	37	0.946			Nov. 13	Table 10	]
	No.874	21	Da ^t	43	44	0.977			Nov. 14	Table 11	1
	No.874	23	Da ^t	8	9	0.889			Nov. 16	Table 12	
	No.874	25	Da ^t	8	14	0.571			Nov. 18	Table 12	
	No.184	15	Sh, Td ^w	7	12	0.583	0.583		Jun. 17	Table 3	
	Hotaru	unknown	Sh, Td", Da', Da'	45	54	0.833	0.859		Jun. 18	Table 4	]
	Hotaru	unknown	Sh, Td', Td ^w	16	17	0.941			Jun. 21	Table 5	]
	Blue	unknown	Sh, Td', Td ^w , Da'	17	18	0.944			Jun. 22	Table 6	
	Blue	unknown	Sh, Da', Da'	22	33	0.667			Jun. 23	Table 7	
	Blue	unknown	Sh, Td ^w , Da ^r , Da ^t , Da ^w	62	86	0.721			Jun.24	Table 8	
2001	B883	16	Sh, Da', Da'	9	11	0.818	0.730	0.763	Aug. 16	Table 9	]
2001	B883	17	Da', Da'	18	26	0.692			Aug. 17	Table 9	this trial
	No.3158	26	Da "	3	10	0.300			Nov. 17	Table 10	
	No.3158	27	non	3 0	5	0.000	0.767		Nov. 18	Table 10	
	No.3158	28	Pi, Td', Da ^w	23	24	0.958			Nov. 19	Table 11	
	No.3158	29	Td ^w , Da ^t , Da ^w	17	18	0.944			Nov. 20	Table 11	
	No.3158	30	Td "	1	1	1.000			Nov. 21	Table 11	
	No.3158	31	Td "	2	2	1.000			Nov. 22	Table 11	
2003	Pink	unknown	Sh, Da', Da'	26	40	0.650	0.680	0.680	Sep. 16	Table 12	
	Pink	unknown	Sh, Da ^t	42	60	0.700	5.000	5,000	Sep. 17	Table 13	
2001	12 visitors			61	207	0.295	-	0.356	Nov. 8	Fig.3	
	9 visitors	17-18	Td', Td ^{**} , Da', Da ^t	42	157	0.268			Nov. 9	Fig.4	this trial
	4 visitors	20	Sh, Td ^w , Da', Da'	11	67	0.164	0.550		Nov. 11	Fig.5	uns una
	7 visitors	20-21	Sh, Td', Td", Da', Da', Da"		111	0.423			Nov. 12	Fig.5	

Table 14. The appearance rate of dance performances (d.p.) in a visitor or visitors at the feeder.

with the feeder at 130 m that No.3104 performed  $Da^{w}$  on Nov. 12, 2001 (cf. Figure 5 lower). However, the waggle dancer Blue first performed  $Da^{t4}$  with the feeder at 60 m, and stably performed  $Da^{t4}$  with the feeder under 40 m (cf. Table 8).

Von Frisch (1967) wrote: "If the feeding place is 10 m from the hive, only round dances are seen (his figure 29); From about 25 to 100 m is the region of transition from round dance to tail-wagging dance; The shift is gradual and may take place in the following way" (his figure 56, upper row of diagram, cf. Table 3). This vague description may be a natural result from such observations as ours on the replacement of  $Da^{14}$  by  $Da^{w}$ . This transition would be influenced by various factors such as wind, temperature, and various barriers, etc.

The behavior of Pink in 2003 was beyond our understanding. It was a riddle that Pink did not perform  $Da^{w}$  but  $Da^{t4}$  with the feeder at 155 m, and performed  $Td^{w}$  alone and did not visit the feeder the next day. Our only idea was the decrepitude or senility of Pink. Her age was inferred to be 40-43 days old, but there is a possibility that she was more senior. Senility may be one of the above inhibitive factors on the appearance of  $Da^{w}$ .

### 3. The dance appearance rate in many visitors

When a researcher believes that it is the fact that honeybee workers get the distance and direction information about a food source from dance performances of nestmates, he could not think of the dance appearance rate (= the number of dance performances / the number of flights). For, the rate must be a usual and near 100 %, if the dance is a mean of communication. We had not felt the importance of this rate until Figures 3-5 were created, when we perceived and were surprised by the low rates. There is first the possibility of underestimation because many dances occur on the comb surface of the observation hive, but the rate is still too low. Therefore, using data of Ohtani (2000, 2002) and this trial, we created Table 14, which shows that many visitors become poor dancers after visiting a crowded feeder. A feeding visitor often flew out when other visitors approached. It is unknown how the poor dancers are related to the 3 shift groups, which seemed alternately to forage at the movable feeder (broken-line borders in Figures 3-5).

In the observation in 2000, 2 foragers, Nos. 862

and 874, simultaneously went to and from the feeder. They often interacted each other, but we cannot assume that the interaction influenced the dance appearance rate (Table 14). If so, No.874 seemed to have been more strongly influenced than No.862 (appearance rate: 0.278 vs 0.536). There may have been aerial interaction in their similar flight course.

In the observation of W1110 in 1999, the appearance rate was considerably lower (0.286). Ohtani (2000) explained this as follows: "When October of 1999 set in, many Japanese giant hornets (*Vespa mandarinia japonica*) made frequent attacks on our apiary." It is conceivable that an incursion of hornets influenced the dance appearance rate.

If the mutual interaction of foragers or hornet incursion would lower the dance appearance rate, Ohtani (2000)'s speculation would be supportable: "when a stable and straight flight course decreases the flight cost, excess energy ... produces a sort of imitation flight." Further investigation of the dance appearance rate would remove the veil of mystery as to why visitors dance on the comb surface, or why not.

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