



Asian hive bees, *Apis cerana*, modulate dance communication in response to nectar toxicity and demand

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Some nectars, such of that of the thunder god vine, *Tripterygium hypoglaucum*, contain alkaloids that are mildly toxic to honeybees, *Apis* spp. Given a choice, foragers prefer nontoxic honey to that of *T. hypoglaucum*, but only if there are no alternative nectar sources. Here we show that foragers of the Asian hive bee collecting *T. hypoglaucum* honey modulate their recruitment dances depending on the availability of alternatives. When alternative nectar sources were available, dancers decreased the frequency of waggle dances and increased the frequency of tremble dances. Furthermore, the waggle dances were less precise than usual. These changes are likely to reduce recruitment. By contrast, when there were no alternative nectar sources available, foragers collecting *T. hypoglaucum* honey performed near-normal dances. Because dance behaviour is dependent on the alternative food sources available, changes in the bees' behaviour is probably not due to the nectar's toxicity per se. We conclude that modulation of in-hive communication serves to protect the colony from death caused by the collection of high quantities of toxic food while preventing starvation when no other food is available.

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A major benefit of group living is the ability of group members to share information about the environment (Lachmann et al. 2000). A group-living animal can use information possessed by other members of its group to decide whether to stay in its current foraging range or to leave for an alternative range that is being advertised by other group members (King & Cowlshaw 2007). Some of the best-known examples of information sharing are found in the social insects, in which many species have evolved complex signalling mechanisms that are used to recruit group members to food sources (Beekman & Dussutour 2009). Of these signalling mechanisms, the waggle dance of honeybees is one of the most sophisticated.

The honeybees' waggle dance encodes both the direction and distance to the advertised source (von Frisch 1967). During a typical dance, the dancer strides forward while vigorously shaking her body from side to side (Tautz et al. 1996). This is known as the 'waggle phase' of the dance. After the waggle phase, the dancing

bee makes an abrupt turn to the left or right, circling back to start the waggle phase again. This is known as the 'return phase'. At the end of the second waggle phase, the dancer turns in the opposite direction so that with every second circuit of the dance she traces the famous figure-of-eight pattern of the waggle dance (von Frisch 1967). Directional information is contained in the angle of the waggle phase, while distance information is encoded in the duration of the waggle phase (von Frisch 1967; Esch et al. 2001). The key components of the waggle dance are summarized in Fig. 1.

Nectar is stored in cells by receiver bees and returning nectar foragers thus need to find nectar receivers upon their return to the colony. When nectar influx is high, an individual forager waits longer until she finds receiver bees (Seeley 1992). Average wait time thus provides returning foragers with an indication of nectar abundance in the colony's environment (Anderson & Ratnieks 1999). When wait times are short, a forager will often attempt to recruit more foragers to her foraging site by performing a waggle dance (von Frisch 1967). When wait times are long, the forager may perform a tremble dance, which discourages foraging (Seeley 1992). A tremble dance is characterized by strong side-to-side shaking of the body, erratic movements of the body axis and slow walking across the comb (von Frisch 1967; Seeley 1992, 1995).

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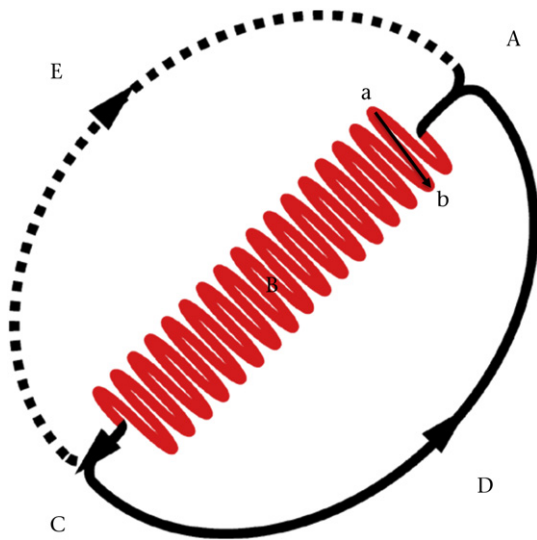


Figure 1. Diagrammatic representation of a waggle dance, indicating the dance characteristics measured in this study. A typical dance proceeds from A to C via B and then returns to A via either D or E. The interval during which the forager vibrates her body from side to side (B) is the waggle phase. The intervals C–D–A or C–E–A are called the return phase. A dancer normally alternates return phases via E and D. The movement from a to b is one waggle. Redrawn from Tautz (2008).

The ability to communicate the location of food sources to nestmates means that the discovery of a profitable food source by just one forager is sufficient to allow a colony to exploit that source rapidly (Seeley & Visscher 1988; Beekman & Ratnieks 2000; Beekman & Lew 2008). But what if the food source is toxic? Alkaloids commonly associated with herbivore defence are present in the nectar of some plant species, so that their nectar is toxic or repellent to most floral visitors (Adler 2000). During periods when there are limited floral resources, honeybee colonies may be obliged to exploit food sources that they would normally ignore (London-Shafir et al. 2003; Liu & Fu 2004; Nicolson & Human 2008). For example, in southern China, during the summer, the Asian hive bee, *Apis cerana*, is forced to forage on the toxic nectar of a perennial vine, *Tripterygium hypoglaucum*, also known as the thunder god vine, because there are limited alternative food sources. Nectar produced by *T. hypoglaucum* contains a terpenoid known as triptolide, which is mildly toxic to bees (Tan et al. 2007). Given a choice, bees prefer nontoxic honey to that of *T. hypoglaucum* (Tan et al. 2007). In addition, honeybee foragers can learn to associate odours with toxic effects (Wright et al. 2010).

We investigated how a honeybee colony regulates the accumulation of toxic honey. We predicted that when foragers foraged on objectionable nectar they would reduce their recruitment behaviour relative to workers foraging on nectar without toxic or objectionable qualities. Changes in dance form might include reduced number of waggle phases per dance, longer return phases between waggle phases, increased frequency of tremble dances and an increased number of errors, as indicated by irregular dance forms and greater variance in the components of the dance (e.g. waggle phase duration and direction; Schneider 1949; Schick 1953).

METHODS

General Procedures

We performed our experiments at the Eastern Bee Research Institute of the Yunnan Agricultural University. To perform an experiment, we placed three *A. cerana* colonies comprising two

combs of bees and brood into observation hives. On each experimental day, we captured about 30 foragers at the entrance of one of the colonies and placed them into individual opaque tubes. We then released the bees one at a time at a feeder placed 130 m from the colony under test. If a released bee began to imbibe food, we colour-marked her until we had individually marked 15 bees. Each day's test started at 1100 hours and lasted over 2 h. We removed all the marked bees from the observation hive under test at the end of each day.

For each colony, we offered one of two food sources at the feeder on alternate days. We used the three colonies in succession until each was tested three times, resulting in nine food type comparisons over 18 days for each experiment. We alternated the position of the feeder each day to avoid interference from bees of the previously tested colonies.

Marked bees were videorecorded after their return into their observation hive, and recordings were subsequently analysed at $\frac{1}{4}$ normal speed.

Experiment 1: *T. hypoglaucum* Versus *Vicia sativa* Honey

We obtained reasonably pure samples of common vetch, *Vicia sativa*, and *T. hypoglaucum* honeys by extracting honey from colonies that were in close proximity to the target species during the appropriate flowering period. In April 2008 (when nectar was plentiful) and May (when there was a nectar dearth) we alternated *T. hypoglaucum* honey (diluted one part honey to two parts water) or common vetch honey, diluted so that it contained a similar amount of dissolved sugar as used in our treatment (measured by a refractometer). Common vetch honey is highly attractive to *A. cerana* foragers. We recorded the in-hive behaviour of the marked bees. From the videos we recorded, for four haphazard bee returns for each of three colonies for each of two food types (i.e. 12 bees per food type): the wait time (time from entering the colony until trophallactic contact with nectar-receiving bee leading to food transfer of a duration >5 s) and the duration of the trophallactic contact upon return to the hive. We further recorded the dance form (waggle or tremble) for all dances performed by any of the 15 marked bees. We recorded each bee's dances only once.

We randomly selected three marked bees per food type and colony (total 18 bees), examined the recordings at $\frac{1}{4}$ speed, and recorded the number of waggle phases per dance, the waggles per waggle phase, the waggle phase duration and duration of the return phases. (A single waggle was assessed as a lateral swing of the abdomen from one side of the body to the other side.) We compared characteristics of dances performed by bees foraging on common vetch and *T. hypoglaucum* honey syrup based on two-way ANOVA of month and food type, with dance nested within colony. Within a food type, we assessed dance precision by calculating the within-dance variance in the duration of waggle and return phases from two-way ANOVA of dance and colony, and used Levene's test of equality of variances to determine if the variance within dances differed between the two types of honey syrup.

When a forager performs a waggle dance, she normally turns alternately to the left or right to begin the return phase at the end of the waggle phase (von Frisch 1967). Deviations from the alternate left and right turns (e.g. two consecutive right turns) appear to be a measure of the 'disorderedness' in the dance. For each of the 18 dances we counted the correct and incorrect turns and compared their frequencies across food types, pooling the data across days and colonies. We also assessed the bees' dance precision by calculating the circular variance (Mardia 1972; Zar 1996) within each dance per bee with respect to the angles of the waggle phase. We compared the circular variances between food types using two-tailed Mann–Whitney *U* tests (Zar 1996).

Table 1
Dance characteristics of bees foraging on *Tripterygium hypoglaucum* or common vetch, *Vicia sativa*, honey

Phenomenon	April 2008 (high natural nectar availability)		May 2008 (low natural nectar availability)		Statistical difference	
	<i>V. sativa</i> honey syrup	<i>T. hypoglaucum</i> honey syrup	<i>V. sativa</i> honey syrup	<i>T. hypoglaucum</i> honey syrup	Between food sources across months	Food*month interaction
Number of waggle dances	11	0	32	28	$\chi^2_1 = 19.17$	Heterogeneity $\chi^2_1 = 8.27$
Number of tremble dances	0	16	0	0	$P < 0.001$	$P < 0.001$
Bees that did not dance	124	119	103	107		
Wait time for receiver bee (s \pm SE)	8.92 \pm 1.55	19.00 \pm 1.55	9.67 \pm 1.55	12.92 \pm 1.55	ANOVA \sqrt{X} $F_{1,44} = 20.12$, $P < 0.001$	$F_{1,44} = 4.77$, $P = 0.034$
Trophallaxis (s \pm SE)	22.41 \pm 1.23	24.50 \pm 1.23	19.25 \pm 1.23	20.83 \pm 1.23	ANOVA $F_{1,44} = 2.24$, $P = 0.14$	$F_{1,44} = 0.042$, $P = 0.84$
Marked bees that returned to the feeder/135	31	7	56	37	$\chi^2_1 = 18.63$ $P < 0.001$	Heterogeneity $\chi^2_1 = 4.93$ $P = 0.027$

Characteristics of communication dances performed by 15 bees per day over 3 days across three replicate colonies (total 135 marked foragers per honey type) when foraging on diluted honey obtained from *V. sativa* and *T. hypoglaucum*. Also shown are the mean (\pm SE) wait times before a returning forager had located a receiver bee for a subset of 12 bees as well as total trophallaxis time. P values in bold are significant at the 5% level after a sequential Bonferroni correction (Rice 1989). Where necessary a square-root transformation was applied to stabilize the variance across groups.

Experiment 2: Triptolide Versus Control

We wondered whether the results obtained in 2008 were due to the bees avoiding accumulating too much *T. hypoglaucum* honey because it is toxic in large quantities, or because the honey is in some other way objectionable. In 2009 we therefore repeated the experiment using 10 μ g/g triptolide (Medical Research Institute, Fujian, China) in 30% w/w sucrose solution and 30% sucrose solution as a control, using the same experimental design and statistical procedures as above. We performed the experiment in May (nectar dearth) and July (extreme dearth). In this experiment we recorded the number of waggle and tremble dances performed by 135 marked bees per food type, and the number that returned to the feeder at least once. We also recorded the dance characteristics of three bees per day, (nine bees per food type as in Experiment 1). We did not record the duration of trophallaxis events or deviations in the waggle phase angles in this experiment.

RESULTS

Experiment 1: *T. hypoglaucum* Versus Common Vetch Honey

When natural nectar was plentiful (April), foragers collecting *T. hypoglaucum* honey never performed waggle dances, but performed some tremble dances (Table 1). When foragers from the same colonies collected common vetch honey, they never performed tremble dances and some performed waggle dances. By contrast, during a nectar dearth (May), returning foragers were quickly relieved of their loads and no tremble dances were performed, irrespective of the honey syrup carried, a significant reversal of behaviour between April (nectar plentiful) and May (nectar dearth; Table 1). Irrespective of natural nectar abundance, workers foraging from a feeder provided with *T. hypoglaucum*

honey were less likely to return than when the feeder had common vetch honey (Table 1). However, proportionally more bees returned to *T. hypoglaucum* honey in May (nectar dearth) than they had in April when nectar was plentiful (Table 1).

We made detailed comparisons of the key features of waggle dances when bees were foraging at *T. hypoglaucum* ($N = 9$ dances from three bees per day across three colonies) and common vetch honey syrup ($N = 9$) when natural nectar was scarce (May). Foragers returning from *T. hypoglaucum* honey performed significantly more dance circuits per dance than those foraging on common vetch honey, although not after Bonferroni correction (Table 2). Other components of the dance, including the number of waggles in the waggle phase, the duration of the waggle phase and the duration of the return phase, were not significantly different between food types (Table 1). However, the waggle dances performed by bees returning with *T. hypoglaucum* honey syrup showed significantly more variation in within-dance characteristics than bees returning with common vetch honey syrup (Table 2). Bees returning with *T. hypoglaucum* syrup had greater variance in the number of waggles in the waggle phase, the duration of the waggle phase and the duration of the return phase (Table 2). Furthermore, the proportion of incorrect turns was significantly greater when bees danced for *T. hypoglaucum* syrup than when they did for common vetch syrup (Fig. 2; $\chi^2_1 = 15.17$, $P < 0.001$). The mean circular variance within dances was significantly greater (Mann–Whitney U test, $U = 2$, $N_1 = N_2 = 9$, $P < 0.001$) when bees danced for the feeder containing *T. hypoglaucum* syrup (0.38 ± 0.26) than when for dances containing common vetch syrup (0.15 ± 0.03). Figure 3 illustrates a typical ordered dance for common vetch honey syrup with a disordered dance for *T. hypoglaucum*, and movies of the different kinds of dances are available in the Supplementary Material.

Table 2
Statistical results of differences in dances between bees dancing for *Tripterygium hypoglaucum* or common vetch, *Vicia sativa*, honey syrup

Dance characteristic	<i>V. sativa</i> honey syrup		<i>T. hypoglaucum</i> honey syrup		ANOVA: means equal across food types	Levene's test of equality of within-dance variance
	Mean \pm SE	Within-dance error mean square	Mean \pm SE	Within-dance error mean square		
Number of waggle runs in the dance	12.89 \pm 1.86	NA	19.44 \pm 1.86	NA	$F_{1,14} = 6.48$, $P = 0.023$	NA
Number of waggles in the waggle phase	9.61 \pm 0.22	2.89	8.09 \pm 0.19	7.20	$F_{1,16.4} = 2.62$, $P = 0.12$	$F_{166,107} = 2.50$, $P < 0.001$
Duration of the waggle phase (s)	0.59 \pm 0.17	0.017	0.57 \pm 0.15	0.045	$F_{1,16.9} = 0.22$, $P = 0.64$	$F_{166,107} = 2.65$, $P < 0.001$
Duration of the return phase (s)	1.38 \pm 0.04	0.19	1.2 \pm 0.036	0.31	$F_{1,16.9} = 1.84$, $P = 0.64$	$F_{166,107} = 1.61$, $P < 0.004$

ANOVA of components of dances performed by nine bees returning from a feeder containing *Tripterygium hypoglaucum* honey syrup or a feeder containing *Vicia sativa* honey syrup. These data were collected in May 2008 when nectar was scarce. Data are from three replicate colonies and three replicate days. P values in bold are statistically significant at the 5% level after sequential Bonferroni correction (Rice 1989).

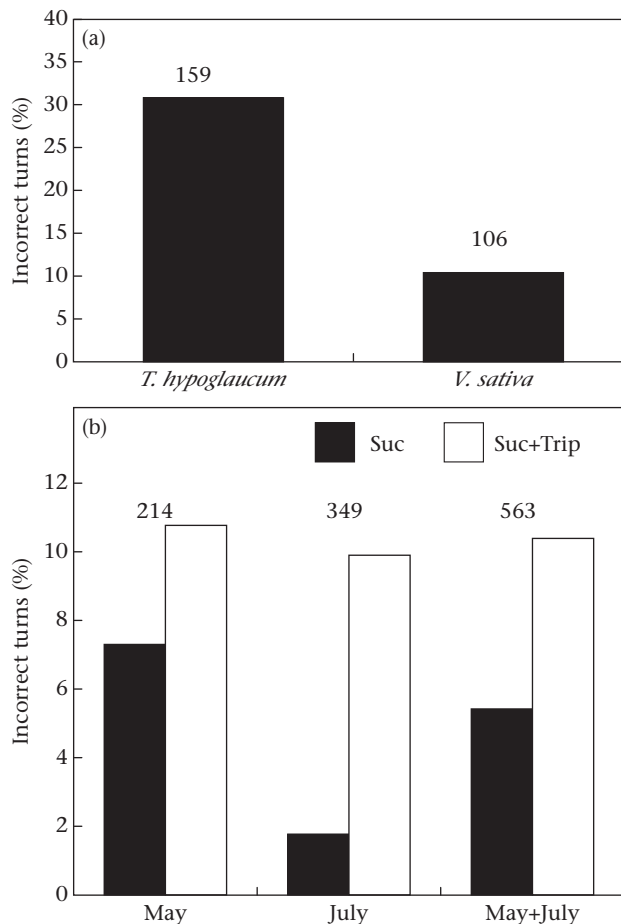


Figure 2. (a) May 2008, nectar dearth. The proportion of incorrect return phases (i.e. where two consecutive turns were in the same direction) in dances of bees foraging on two alternative food sources. The numbers above the bars are the total number of turns scored. Foragers dancing for *T. hypoglaucum* or common vetch, *V. sativa*, honey syrup. (b) May (nectar dearth) and July (extreme nectar dearth) 2009. Foragers dancing for 30% sucrose syrup (Suc) or sucrose syrup with 10 µg/g triplotide (Suc + Trip), thought to be the toxic component of *T. hypoglaucum* honey.

Experiment 2: Triplotide Versus Control

We did not observe any tremble dances among the 135 bees foraging on sugar syrup even when it contained triplotide. The presence of triplotide in food had no significant effect on the proportion of bees that performed waggle dances in either May (nectar dearth) or July (extreme nectar dearth), but significantly

fewer bees returned to the feeder when the syrup contained triplotide, irrespective of month (Table 3).

When data were pooled across food types, there was no significant effect of month on any of the measured components of the dances (Fig. 4). However, the presence of triplotide in the food had significant effects on the behaviour of dancers that varied by month (Fig. 4). The number of circuits per dance was significantly reduced when bees returned from the feeder containing triplotide (Fig. 4; $F_{1,30} = 6.8$, $P = 0.014$, ln transformed data), with a significantly greater reduction in May (nectar dearth) than July (extreme nectar dearth; Fig. 4; month * food interaction: $F_{1,30} = 4.28$, $P = 0.047$). The duration of the waggle phase of dances was significantly reduced by triplotide in May, but increased in July (Fig. 4), resulting in a highly significant month by food interaction ($F_{1,606} = 20.58$, $P < 0.001$). None the less, the variance in the duration of the waggle phase within dances was similar, irrespective of the presence of triplotide in the sucrose syrup (Table 4).

The number of waggles in each waggle phase was reduced by triplotide in May (nectar dearth) but not in July (extreme nectar dearth; Fig. 4), leading to a highly significant month * food type interaction ($F_{1,606} = 40.90$, $P < 0.001$). The within-dance variance in the number of waggles per run was increased in bees feeding on triplotide syrup in May but not in July (Table 4). Similarly, the duration of the return phase was increased when bees returned from the triplotide-containing feeder in May, but not in July (Fig. 4), although here the month * food type interaction was not significant ($F_{1,567} = 1.96$, $P = 0.16$). The within-dance variance in the return phase was significantly greater in bees dancing for triplotide-spiked syrup in both months (Table 4).

There were significantly more incorrect turns in dances performed by bees feeding on sucrose + triplotide across both months (Fig. 2; $\chi^2_1 = 4.87$, $P = 0.03$), and the effect was similar in both May and July (heterogeneity $\chi^2_1 = 3.04$, $P = 0.08$).

DISCUSSION

Our experiments suggest that *A. cerana* foragers change their dance behaviour in response to objectionable components in nectar, as has been previously noted in the European honeybee, *Apis mellifera* (Schneider 1949; Schick 1953), but that the bees modulate these changes in response to the availability of alternatives. When nectar is scarce, foragers dance for food that they would normally avoid, and with similar enthusiasm (as measured by similar return phase durations; Seeley et al. 2000) for attractive and unattractive sources of food. When alternatives are available, bees foraging on objectionable food perform fewer waggle dances, perform dances with greater within-dance variability, and with

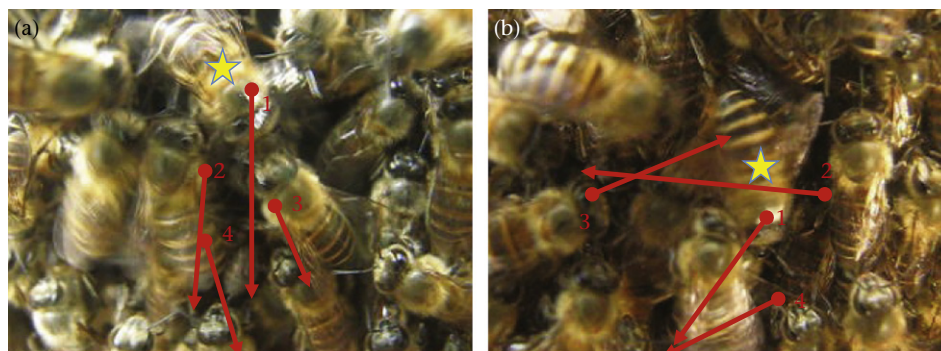


Figure 3. Typical dances of bees dancing for (a) the control feeder and (b) the feeder containing *T. hypoglaucum* honey. Directional information is conveyed in the waggle phase. The bees marked with a star finished four waggle phases, shown here as red arrows. The bee in (a) performed directional dances, whereas the bee in (b) performed undirectional dances.

Table 3
Dance behaviour of bees foraging either at sucrose with triptolide or without

Phenomenon	May 2009 (low natural nectar availability)		July 2008 (almost no natural nectar availability)		Statistical difference	
	30% sucrose	Sucrose+10 µg/g triptolide	30% sucrose	Sucrose+10 µg/g triptolide	Between food sources across months χ^2_1	Heterogeneity χ^2_1 food* month interaction
Number of waggle dances	39	34	52	44	1.46 $P=0.23$	0.047 $P=0.83$
Bees that did not dance	96	101	83	91		
Marked bees that returned to the feeder/135	66	38	87	69		

Behaviour of 15 foragers per day over 3 days across three replicate colonies (total 135 marked foragers per treatment) when foraging on 30% vol/vol sucrose syrup and sucrose syrup containing 10 µg/g triptolide. The P value in bold is significant at the 5% level after a sequential Bonferroni correction (Rice 1989).

more tremble dances. In sum, a colony trades off its need for food with its need to avoid food with toxic components.

The bees clearly indicated that they preferred common vetch honey syrup over *T. hypoglaucum* syrup, with lower return rates, lower probability of waggle dances, increased probability of tremble dances, reduced number of waggles in the waggle phase and longer return phases in dances for *T. hypoglaucum*. However, when natural nectar was scarce, the proportion of foragers that danced for *T. hypoglaucum* approached that for common vetch, strongly suggesting that the bees modulated their dance behaviour depending on the availability of alternative nectar sources.

The reversion to normal dance forms when alternative food sources were unavailable indicates that the disordered dances observed when at least some natural nectar is available is probably not caused by the toxicity of *T. hypoglaucum* honey per se. Rather it seems that returning foragers may only be willing to advertise the food source (via a waggle dance) if they are unloaded quickly. The disordered dance patterns, characterized by irregular left/right turns at the end of the waggle phase and increased within-dance variance, may be interpreted as a transitional dance form between a waggle and a tremble dance, suggesting that the tremble dance is closely related to the waggle dance, but lacks the forward stride typical of waggle dances. This form of dance may be typical when a food source is abundant but

in some way objectionable. We note that irrespective of whether the foragers modulate their dances when alternatives are available, or whether the change arises directly from toxicity owing to longer unloading times, the effect is the same at the colony level: there will be fewer recruits to the toxic nectar when alternatives are available.

Our experiments using triptolide, thought to be the toxic component of *T. hypoglaucum*, largely confirm those performed with the actual toxic honey. The bees indicated that they preferred the triptolide-free syrup by lower return rates and higher within-dance variance. In May (nectar dearth), bees foraging on syrup containing triptolide had shorter waggle phases and fewer waggles per waggle phase than bees foraging on syrup without triptolide. Shorter waggle phases indicate that the food source is closer to the colony (von Frisch 1967), but is unrelated to perceived profitability (Seeley et al. 2000; Shafir & Barron 2010). Why the perception (or advertisement) of distance should change with the presence of toxin is unclear to us. We note that the difference in waggle phase duration between nectar with and without toxin disappeared when there was a complete dearth of nectar (July). However, foragers still indicated that sucrose solution containing triptolide was objectionable by more variable return phases, reduced circuits per dance and higher variance of within-dance components. This may be a manifestation of the forager's trade-off of enthusiasm for the food

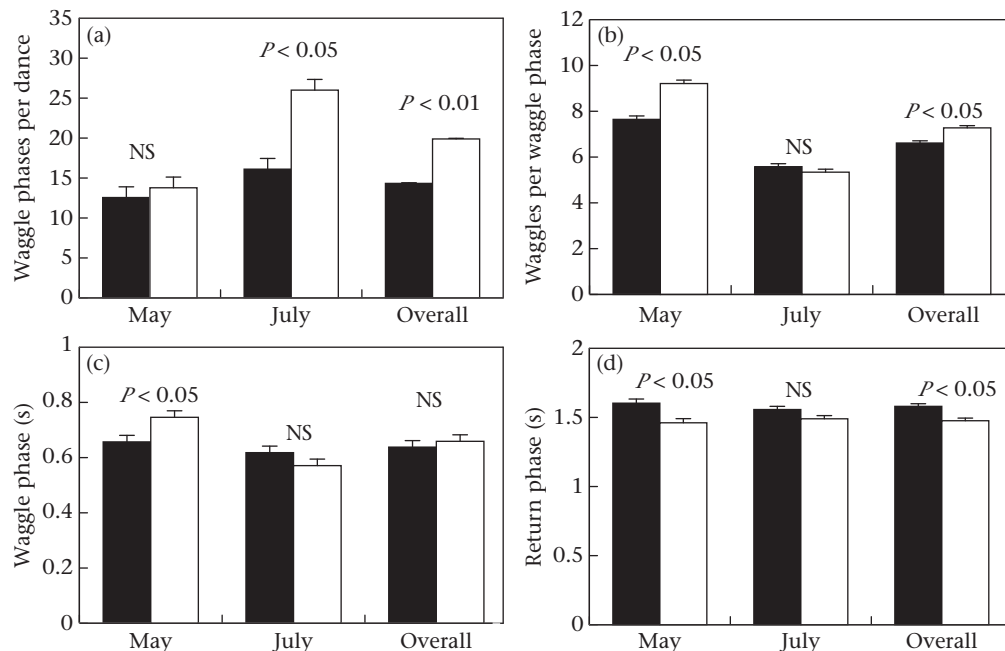


Figure 4. Mean measures on selected components of the dance language performed by bees foraging on 30% sucrose syrup (white) and 30% sucrose syrup supplemented with 10 µg/g triptolide (black) in May (nectar dearth) and July (extreme nectar dearth). Tests of the effect of month pooled across food types are as follows: circuits per dance $F_{1,11} = 3.3$, $P = 0.32$; waggles per waggle phase: $F_{1,11} = 10.80$, $P = 0.19$; waggle phase duration $F_{1,11} = 2.48$, $P = 0.36$; return phase duration: $F_{1,11} = 0.049$, $P = 0.86$.

Table 4
Statistical results of differences in dance behaviour between bees foraging at sucrose with triptolide or without

Dance characteristic	May		Levene's test of equality of variance	July		Levene's test of equality of within-dance variance
	Within-dance error mean square			Within-dance error mean square		
	Sucrose	Sucrose+triptolide		Sucrose	Sucrose+triptolide	
Duration of the waggle phase (s)	0.015	0.020	$F_{106,105}=1.33$, $P=0.065$	0.23	0.24	$F_{136,225}=1.04$, $P=0.39$
Waggles per waggle run	1.86	3.85	$F_{106,105}=2.07$, $P<0.001$	1.22	1.31	$F_{136,225}=1.07$, $P=0.32$
Duration of the return phase (s)	0.050	0.095	$F_{94,106}=1.92$, $P=0.0007$	0.050	0.096	$F_{127,216}=1.92$, $P<0.001$

ANOVA was used to estimate within-dance variance for various components of dances performed by nine bees returning from a feeder containing 30% vol/vol sucrose syrup or sucrose syrup containing 10 µg/g triptolide. These data were collected in May 2009 when nectar was scarce and July 2009 when natural nectar was almost absent. Data for each month are from three replicate colonies and three replicate days. *P* values in bold indicate significantly different within-dance variance between food types at the 5% level after Bonferroni correction (Rice 1989).

and its learned aversion to the toxin via a separate neural pathway (Wright et al. 2010).

We are not the first to show that honeybees adjust their foraging behaviour in the presence of plant alkaloids in response to the availability of alternative forage, although we are the first to show this in a species other than *A. mellifera*. Nicotine, a naturally occurring alkaloid, is toxic to most herbivores and thus serves as an effective deterrent to herbivory. *Apis mellifera* will forage on sucrose syrup containing nicotine provided that it has a high sucrose content and no alternatives are available (Köhler et al. 2012). Trace elements in nectar influence the bees' perception of nectar profitability and thus affect dance variables and recruitment to the nectar source (Afik et al. 2008). When flowers are considered dangerous owing to the presence of predators, experienced foragers are less likely to perform waggle dances, thus steering recruits away from potentially dangerous sites (Abbott & Dukas 2009).

Our study contributes to the growing body of work elucidating the intricate ways in which honeybees use the dance language to achieve nuanced outcomes. During foraging, the dancer integrates information about patch profitability relative to other patches currently being exploited by the colony as well as the colony's needs. The dance is used to recruit bees to water sources (von Frisch 1967; Seeley 1995) and potential nest sites (Seeley 2010). In species in which the quality of the new nest site is essential for colony survival, the dance reflects the quality of the site found by the scout bee (Seeley 2003), but not so in species that can nest almost anywhere (Makinson et al. 2011).

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2012.09.037>.

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