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Supplementary Materials for

Honeybees forage more successfully without the "dance language" in challenging environments

R. I'Anson Price*, N. Dulex, N. Vial, C. Vincent, C. Grüter

*Corresponding author. Email: r.iansonprice@gmail.com

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Supplementary Materials

Methods

What are oriented and disoriented dances? (E1 and E2)

Oriented dances were dances in which at least 80% of the waggle runs were within 45° of each other. We did not look at the distance information in dances.

Experiment to test the effect of light on the first frame on foraging activity (E3)

The experiment was conducted in two separate periods: August - September 2016 and May - June 2017. Eight colonies were used with frames in a vertical orientation (fig. S1b), either with or without light on the first frame. Bees exiting the colony were counted for 60 seconds between 9am and 10am and between 5pm and 6pm. After 18 days of data collection in a treatment, the colony was put in the reverse treatment for 18 days. Fixed effects were day and treatment (light or dark). Random effects were colony and period (2016 or 2017).

Fig. S1. Hive in horizontal orientation and hive in vertical orientation, both with glass windows. No experiments directly compared these two orientations. Photo: Christoph Grüter, Johannes Gutenberg University Mainz.

Experimental procedure E1

Table S1. Colony treatment order—numbers represent colony ID. In E1 each treatment contained four colonies per experimental period. When treatments were switched, each group of four was split into two groups of two and these were separated into the two other treatments for the experimental next period (Table S1).

Experimental period 1			Experimental period 2			Experimental period 3		
Disoriented	Oriented	Switch	Disoriented	Oriented	Switch	Disoriented	Oriented	Switch
8	3	4	3	8	11	4	18	8
15	17	7	17	15	2	7	13	15
11	20	18	18	4	20	20	11	3
2	19	13	13	7	19	19	2	17

Foraging activity collection

We measured colony activity by taking the weight loss of the colony in the morning using the scale. To confirm this was an accurate measure for colony foraging activity we tested for a correlation of colony foraging activity data with manual counts taken throughout the experiment. Scale foraging activity correlated with the manual count average daily foraging activity (Pearson's product moment correlation; $p < 0.001$, $r^2 = 0.64$ (fig. S2)).

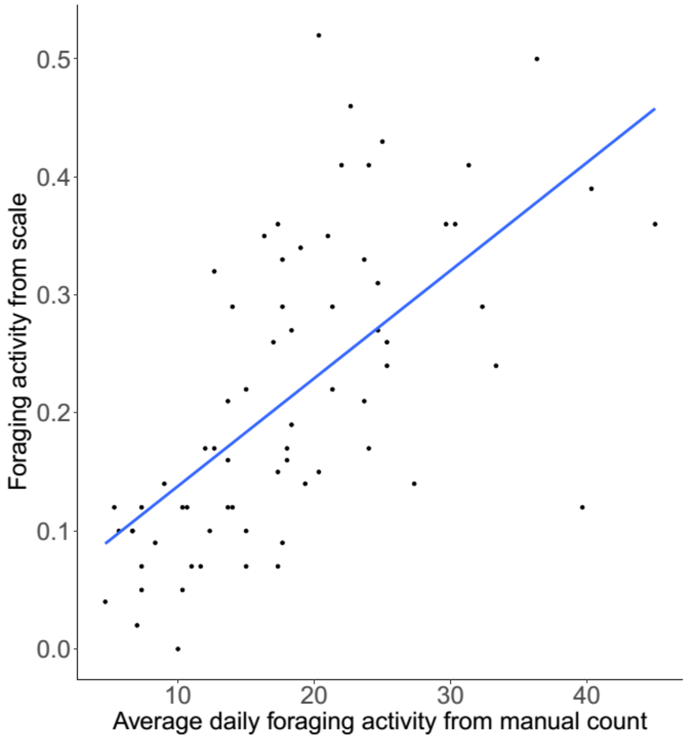

Fig. S2. Correlation of scale foraging effort against morning manual foraging counts.

Nectar collection (E1)

This data was collected from colonies in the 18-day oriented and disoriented treatments. Collection took place on the 9th or 10th day of experiments. The collection was carried out one colony at a time, switching between treatments on a day. Nectar was collected from all colonies on a collection day. Collection started at 10:00 and was finished by 12:00. The bees were collected at the hive entrance after blocking the entrance to stop exit and entry. Around 10 returning foragers were collected per colony. Once all bees were collected from a colony they were placed in labelled bags and put on ice. They were then immediately taken for nectar quality assessment.

Pollen collection (E1)

Pollen was collected from colonies in the 18-day oriented and disoriented treatments. Collection took place on the 8th, 10th, 13th, and 16th day - one colony from each treatment on a day. Collection occurred for 30 minutes from 2pm - 4pm, one time per colony per experimental period. Once collected all grains in a sample were dried, weighed and counted.

Behavioural observations (E1)

When carrying out scan samples on the number of dances, counts started on the side of the window furthest from the entrance. Over 30 seconds the scan slowly moved across the window. As many dances as possible were filmed to completion over a 10 minute period. Dance completion was when a dance stopped and did not restart for more than 5 seconds. After all colonies were scanned, scan sampling was then repeated in the same way as the first count. The video data were used to assess the orientation of dances and check that the oriented treatment had oriented dancing and the disoriented treatment had disoriented dancing. The number of followers that were forced to stop following because the dancer stopped dancing was compared between treatments, but no significant difference was seen (proportion forced to stop in disoriented = 0.02; proportion for to stop in oriented = 0.05; Chi-sqare test: $\chi^2 = 1.55$, $p = 0.21$).

Model description

Entities, state variables and scale

This model is based on a model published by Schürch and Grüter (29). Our agents were located on a two-dimensional square grid with 201x201 patches. The agents' nest was located on the center patch. Every other patch on the grid could either be void or contain suitable forage for our agents. Food patch quality was variable (Table S1) and each patch lasted for a limited number of days. Each colony contained 300 agents ($N_{default}$ = 300) that were either scouts or recruits. Agents designated as scouts search for food source locations without having followed waggle dances and have a high probability to abandon even rewarding food sources and search for new ones. Scouts could exist in any of six states: idle in the colony, scouting for food sources, feeding at a food source, returning to the colony, recruiting of idle foragers to the newly discovered food source, returning to the nest without having discovered food. Recruits followed and decoded waggle dances to find a food patch, but could also scout

(Table 1) if they were unable to find a dancing bee (33). Recruits could adopt any of 8 states: idle in the nest, idly waiting to be recruited, flying to food source, feeding on food source, returning to colony after feeding, recruiting new idle foragers, scouting for forage, returning to the colony without having discovered food. As in Schürch and Grüter (29), simulations were run in discrete time steps with model parameters (Table 1) kept the same for each simulation. Patch sizes and foraging mechanics were the same as in (29).

Process overview

In total, each simulation run lasted 18 days, or 181,440 time steps. At the start of each morning, idle scouts left the nest with a probability p_{Exit}, and idle recruits, waiting for food locations to be communicated to them (dances), left the nest with a probability p_{RS} and started scouting. As in (29) we made p_{Exit} relatively high, this meant scouts left the hive early in the morning. Successful scouts or scouting recruits would feed on patches that offered forage, and then returned to the nest. Having unloaded their forage, they could communicate the location of this food source using the dance to N_{Dance} recruits. The probability of a recruit learning the location of a food source and flying there was p_{Dance}. One recruit could follow each dance (N_{Dance} = 1) and each dance had a 25% probability to recruit a forager to the advertised food patch (p_{Dance} = 0.25) (27, 28, 43). The probability of a forager performing a dance p_d depended on the quality of the visited patch q_{Patch} and the distance to this patch. It also depended upon the influx of foragers: a higher influx of foragers decreased the probability of a bee dancing (21) (see figs. S1 and S2 in (29)). Scouts and recruits became idle once finished with dancing, from which state they could then leave the nest again with p_{Exit}. Scouts searched for new food sources, while recruits, depending on the food source quality and distance, would re-visited previous food patches for the rest of the day or until they died (see fig. S1 in (29)).

Each morning, recruits with foraging experience decided whether to continue visiting the food source they had been visiting on the previous day, if they did not continue they became idle recruits. The probability of a recruit abandoning a food source depended on the quality, as well as on the distance to the patch. If they did not abandon the patch, they left the nest with the probability p_{Exit}. If, overnight, the patch had vanished, the recruits returned to the nest and became idle recruits.

At each time step, agents had a probability of m to die. If an agent died, a completely equivalent new agent was born in the nest. This agent lacked foraging experience, and started out as an idle scout or recruit. Each day forage patches with an age that exceeded a_{max} were replaced by empty patches. Empty patches could become forage patches with a probability d_{Patch} and quality q_{Patch}.

Table S2. Overview of all model parameters and the values used in our simulations for the two conditions (colonies with dancing or without dancing).

	Dancing	**Scouting**
Number of scouts in the agent population (N_{scouts})	30	30
Number of recruits in the agent population ($N_{default}$)	270	270
Probability of a scout to leave the nest per time step (p_{Exit})	0.815	0.815
Probability that idle recruits will leave the nest and scout per time step (p_{RS})	0.00009	0.25
	Default	**Other values tested**
Density of patches (d_{Patch})	0.01	0.1
Mean patch molarity (q_{Patch})	0.5mol	1mol
Maximum age of patches (a_{max})	5	10, 15

Yield of a foraging trip (y_{Patch})	25 mg 50 mg
Probability of dance success (p_{Dance})	0.25
Nectar handling time in the nest (t_{Nest})	180 ± 60 time steps
Mean ± SD nectar handling time on patch ($t_{Patch} \pm SD_t$)	Mean ± SD nectar quality

Results

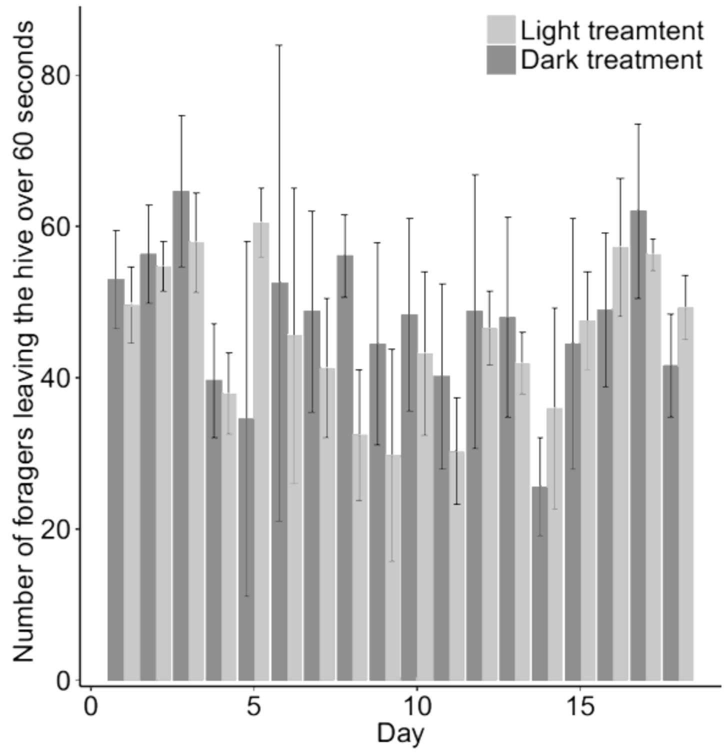

Fig. S3. Test for effect of light on the first frame of vertical colonies. Forager traffic out of the colony over 60 seconds. Mean ± SE are shown. Eight colonies were used in a paired experiment. Counts for a colony on a day were taken at 10am, 2pm and 4pm, this score was averaged for a colony.

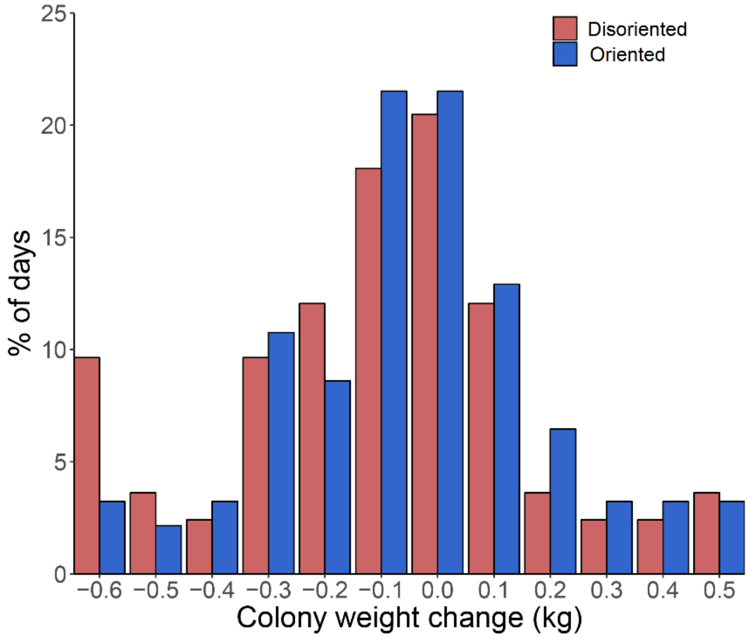

Fig. S4. Daily weight change of hives that were switched every 3 days.

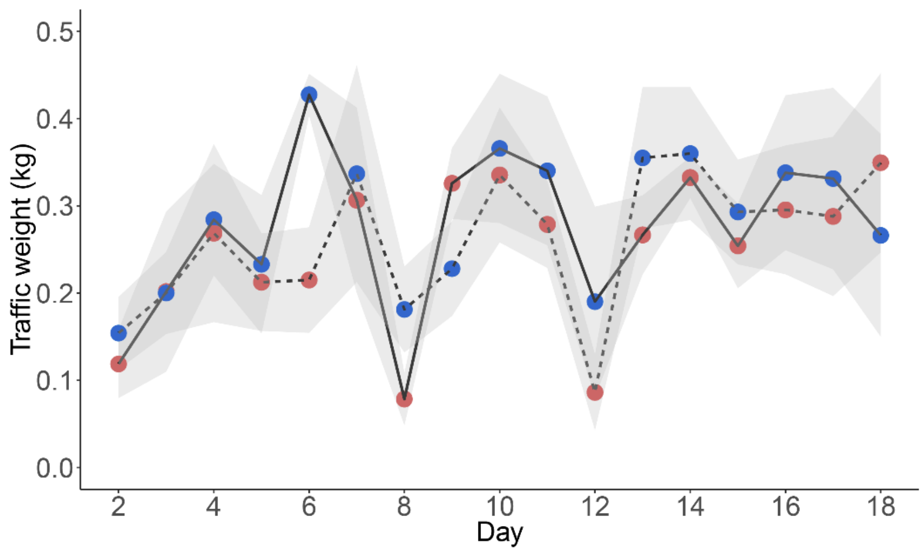

Fig. S5. Foraging activity in hives that were switched every 3 days. Mean ± SE are shown as shaded area.

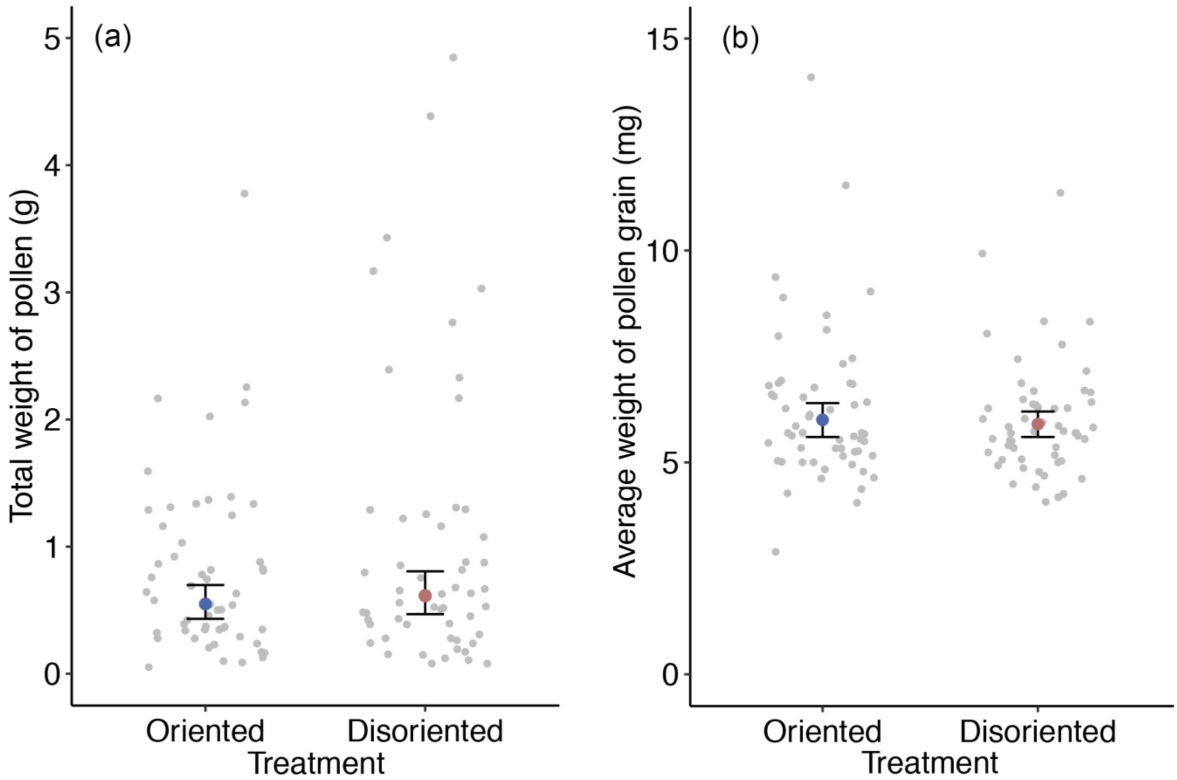

Fig. 6. Colony pollen collection in 18-day treatments. (a) Average weight of total pollen collected in the 30-minute collection period in the two 18 day treatments (geometric mean ± CI). **(b)** Average weight of each pollen grain collected in the two 18 day treatments (geometric mean ± CI). Total weight of pollen was calculated and divided by the total number of grains.

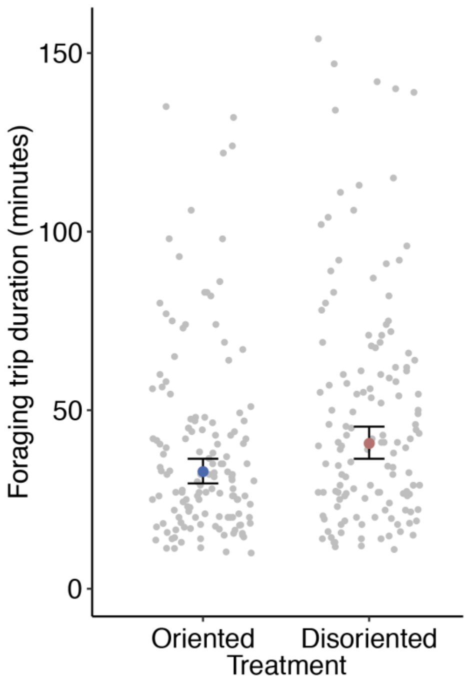

Fig. S7. Foraging journey time of foragers in the 18-day treatments (geometric mean ± CI). Journeys less than 10 minutes were considered to be for water collection or orientation flights and were therefore excluded. Pink points show raw data and size signifies frequency of a particular foraging time.