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A Method for Studying Social Signal Learning of the Waggle Dance in Honey Bees

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Abstract

Honey bees use a complex form of spatial referential communication. Their waggle dance communicates to nestmates the direction, distance, and quality of a resource by encoding celestial cues, retinal optic flow, and relative food value into motion and sound within the nest. This protocol was developed to investigate the potential for social learning of this waggle dance. Using this protocol, we showed that correct waggle dancing requires social learning. Bees (*Apis mellifera*) that did not follow any dances before they first danced produced significantly more disordered dances, with larger waggle angle divergence errors, and encoded distance incorrectly. The former deficits improved with experience, but distance encoding was set for life. The first dances of bees that could follow other dancers had neither impairment. Social learning, therefore, shapes honey bee signaling, as it does communication in human infants, birds, and multiple other vertebrate species. However, much remains to be learned about insects' social learning, and this protocol will help to address knowledge gaps in the understanding of sophisticated social signal learning, particularly in understanding the molecular bases for such learning.

Key features

- It was unclear if honey bees (*Apis mellifera*) could improve their waggle dance by following experienced dancers before they first waggle dance.
- Honey bees perform their first waggle dances with more errors if they cannot follow experienced waggle dancers first.
- Directional and disorder errors improved over time, but distance error was maintained. Bees in experimental colonies continued to communicate longer distances than control bees.
- Dancing correctly, with less directional error and disorder, requires social learning.
- Distance encoding in the honey bee dance is largely genetic but may also include a component of cultural transmission.

Keywords: Honey bee, Waggle dance, Referential communication, Social learning, Experience

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Background

Social learning, the process of learning by observing or interacting with others, is crucial for complex behaviors and adapting these to specific environmental circumstances (Leadbeater and Chittka, 2007). Honey bee workers learn resource location and quality through the waggle dance, a sophisticated form of spatial referential communication (von Frisch, 1967). However, it was unknown if dance following could improve the performances of young waggle dancers or if the dance was entirely innate. Prior research and protocols focused on describing the waggle dance in experienced or novice bees but did not deprive them of the ability to follow waggle dances before they first danced. This deprivation, in which honey bees were unable to use social learning of waggle dancing, has not previously been described as a protocol or used to investigate waggle dancing.

Our protocol, therefore, explains how to design an experiment in which bees cannot follow other waggle dancers before they begin to dance (Dong et al., 2023). These findings indicate that social signal learning can enhance the accuracy of the waggle dance. When compared to bees that were exposed to waggle dancing, naive bees that could not observe dances prior to their first dance displayed larger divergence angle errors, signaled longer distances, and demonstrated significantly more disarray in their dances. However, when these same bees were 20 days old and had gained experience with dance following and dancing, they noticeably reduced divergence angle errors and performed more coordinated dances. Despite these improvements, they were consistently unable to accurately encode distance. These corrections in the experimental older dancers, as compared to their first dances, could be attributed to increased age, more experience following dances, additional practice with flight and foraging, or a combination thereof. Control bees only managed to reduce distance errors as they aged. Having the opportunity to observe experienced dancers before their first dance was enough for the control bees to have the lower directional errors characteristic of older, experienced bees (Dong et al., 2023).

This setup can be employed by other researchers to further explore the role of social learning in eusocial insects and its impact on communication and decision-making within colonies. Such experiments can provide a foundation for designing studies that investigate various aspects of social learning, including the following:

1. Comparisons across species: by conducting similar experiments on different species of eusocial insects, researchers can compare the extent and mechanisms of social learning between species, as well as the influence of genetic and environmental factors on the development of complex behaviors and communication.
2. Impact of social learning on colony performance: researchers can investigate the relationship between the quality of social learning and the overall performance of the colony, including foraging efficiency, resource allocation, and reproductive success. This can help to identify the benefits of social learning in colony organization and decision making.
3. Development of individual learning abilities: by manipulating the availability of social learning opportunities, researchers can study the development of individual learning abilities in eusocial insects and determine the importance of social learning in the acquisition and refinement of specific skills.
4. Neural and molecular mechanisms: investigating the neural and molecular mechanisms underlying social learning in eusocial insects can help to elucidate the cognitive and physiological processes that facilitate the acquisition of complex behaviors and communication strategies.
5. Social learning and colony adaptation: by examining the impact of social learning on the ability of colonies to adapt to changing environments, researchers can better understand the role of social learning in the evolution and resilience of eusocial insect societies.
6. Artificial intelligence and robotics: insights gained from studying social learning in eusocial insects can be applied to the development of artificial intelligence and swarm robotics in which decentralized decision-making and communication strategies are crucial for efficient problem-solving and adaptation.

By using this experimental setup as a starting point, researchers can expand our understanding of social learning in eusocial insects and its broader implications for evolution, ecology, and technology.

Location and timing

The following are instructions on the location and timing of the experiments:

1. Experiments were carried out at the Southwest Center for Biological Diversity, Chinese Academy of Sciences (Kunming, China). These experiments can be conducted at multiple different locations that support healthy *Apis mellifera* colonies.
2. Carry out the experiments during the months of April–June when conditions are good. Note that these months were chosen because the temperature differences between day and night are moderate and facilitate the survival of young bee colonies. The correct months to conduct such experiments will vary depending on local conditions.

Materials and reagents

Biological materials

Ten *Apis mellifera* colonies (five control and five experimental) at a bee apiary. Queens from all colonies should be obtained from the same breeder to ensure greater genetic uniformity.

Materials

1. Graduated cylinder, 1,000 mL (Fisher Scientific™, catalog number: 08-559GC) or volumetric flask with seal, 1,000 mL (Fisher Scientific™, catalog number: 10-200G) (includes the flask and seal)
2. Parafilm™ wax sheet (Bemis™ PM999, Fisher Scientific™, catalog number: 13-374-12)

Reagents

1. Sucrose
2. ddH_2O
3. Sucrose solution (see Recipes)

Recipes

1. **Sucrose solution**

Reagent	Final concentration	Quantity
Sucrose (100%)	55% (w/v)	55 g
ddH_2O	n/a	n/a
Total	n/a	100 mL (final volume)

a. To make a standard 55% (w/v) sucrose solution, weigh out 55 g of reagent-grade sucrose with an electronic balance.
b. Add the sucrose to a graduated cylinder or volumetric flask and then double-distilled water (ddH_2O) until reaching a volume of 75 mL. You may also use distilled water.
c. Shake the vessel to dissolve the sugar. For a graduated cylinder, cover the opening with a Parafilm wax sheet and carefully invert it multiple times to dissolve. For a volumetric flask, use the seal that comes with the flask to seal the flask and then invert the sealed flask multiple times.
d. Add more ddH_2O until the total volume is 100 mL.
e. The water should be freshly obtained but does not have an expiration date if it comes from a sterile, sealed container.
f. Similarly, the dry sucrose does not have an expiration date, provided that the manufacturer's expiration date is not exceeded.
g. It is recommended to prepare this solution freshly each day and use it at room temperature (21 °C). Over time, this sucrose solution can begin to grow mold.
h. If necessary, the prepared solution can be kept at 4 °C for 24 h. Discard after 24 h.

Equipment

1. High-definition video camera (HDR-PJ790, Sony)
2. Incubator (PRX-250B, Ningbo Saifu Experimental Instrument Co., Ltd., https://www.chem17.com/product/detail/37456106.html)
3. Aspirator to capture bees (custom-made):
    a. A manual aspirator is best because the suction can be controlled by a user.
    b. To make such an aspirator, take a clear plastic cylindrical container that is 14 cm in diameter with a removable lid. Drill the lid to add two holes, spaced 10 cm apart and 1 cm in diameter.
    c. Obtain two pieces of clear vinyl tubing that are 1 cm in outer diameter. The mouthpiece tube should be 30 cm long and the bee collection tube should be 60 cm long.
    d. To prevent aspirating the bee into the user's mouth, take a fine stainless-steel mesh and attach it with a 1 cm diameter hose clamp to the tube once it has been inserted through the lid into the collection container.
    e. Take another hose clamp and similarly attach it to the bee collection tube once it has been inserted inside the lid. The clamps will keep the tubes from pulling out the lid.

Software and datasets

1. Tracker software (V4.91) runs on Windows, MacOS, and Linux operating systems and is free. This software is built on the Open Source Physics (OSP) Java framework and is designed for educational use. The software can be downloaded at this website: https://physlets.org/tracker/
2. We used JMP Pro V16.1.0 to analyze our data. A free 30-day trial of JMP is available. This software can be downloaded from this website: https://www.jmp.com/en_us/home.html

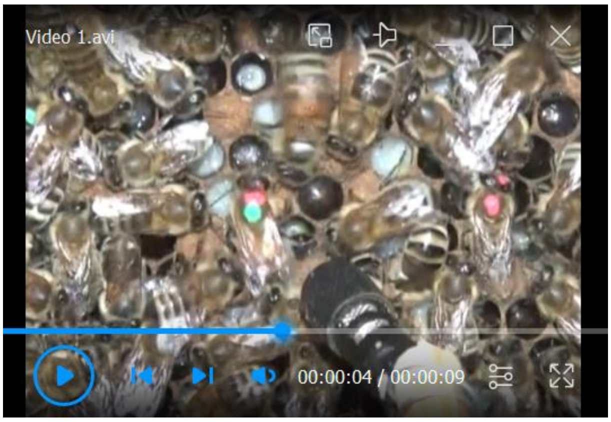
Procedure

A. Creating colonies

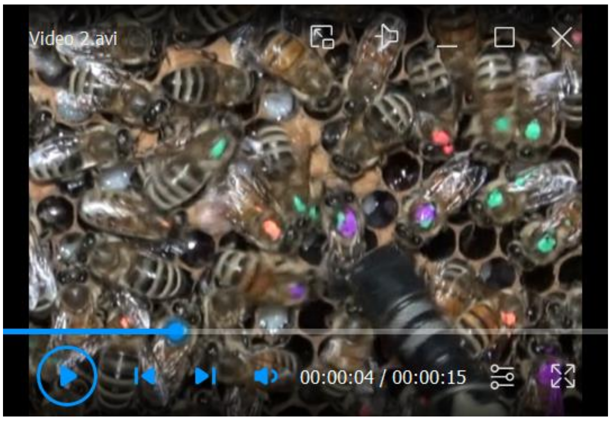
1. You will be creating pairs of colonies (one control and one experimental) from the same source colony to ensure that each pair of colonies has the same genetic background.
2. Control and experimental colonies should have very similar levels of food stores.
3. It is important that all bees (control and experimental) experience the same incubator conditions to account for the potential effects of incubation on bee development and behavior.
4. Each observation hive consists of two combs (43.5 cm × 23 cm)—one frame of brood and one frame of honey and pollen—and is connected by a 2.2 cm inner diameter and 25 cm long tube through the wall to the outside.
5. Creating the experimental colony:
    a. Remove combs with late-stage pupae from haphazardly selected large, healthy colonies.
    b. Place the combs inside a nuc box (standard honey bee nucleus box) inside an incubator for 24 h.
    c. Maintain the incubator in a dark environment with a temperature of 34 °C and a relative humidity of 75%.
    d. Transfer 2,800 one-day-old bees that emerge to a two-frame observation hive with a new egg-laying queen.
    e. Mark 200 of the one-day-old bees with a paint pen. You will track these bees in the experiment.
    f. Ensure that the experimental colonies contain no eggs or brood but only the queen, 2,800 newly emerged bees (of which 200 are marked), and approximately a half comb of pollen and a half comb of honey.

6. Creating the control colony:
    a. Take the source colony and place one comb with late-stage pupae into a nuc box in the same incubator for 24 h.
    b. Maintain the incubator in a dark environment with a temperature of 34 °C and a relative humidity of 75%.
    c. Mark 200 of the one-day-old bees that emerge with a paint pen. You will track these bees in the experiment.
    d. At the same time, take 2,600 bees of all ages and, likewise, place them on combs in a nuc box in the same incubator for 24 h under the same conditions.
    e. Transfer the 2,800 one-day-old bees to a two-frame observation hive with a new egg-laying queen.
7. Repeat as needed to create five experimental colonies and five control colonies that derive from five original source colonies.

These videos illustrate the waggle dances of control bees (Video 1) that exhibit normal levels of error and the waggle dances of experimental bees that did not have the opportunity to follow other dancers before they first danced and therefore show higher levels of error (Video 2). Video files may be downloaded or viewed at the following links. Downloading will usually enable the viewer to see the video at a higher quality.



Video 1. First waggle dance of a bee from a control colony that was able to follow other dancers before performing its first waggle dance (orange and green paint on thorax)



Video 2. First waggle dance of a bee from an experimental colony that was never able to follow another waggle dancer before performing its first waggle dance (green and purple paint on thorax)

B. Monitoring first waggle dances with no prior experience

1. Observe all colonies every day during daylight hours until the first bees fly out to forage.
2. Train these foragers to a 55% (w/v) sucrose feeder placed 150 m from the colony.
    a. Choose locations such that a direct flight path from the colony to the feeder results in bees from each colony experiencing similar levels of optic flow (see this example of our field site: https://map.bmcx.com/ciba__map/).
    b. Ensure that feeders are placed on a grass field with similar local landmarks (similar buildings and trees) at each feeder site.
3. Create feeders consisting of a 70 mL vial (8 cm high) inverted over a circular plastic disk with 18 feeding grooves through which the sucrose can flow.
    a. Fill the vial with sucrose solution, then invert on the plastic disk and place over a piece of colored paper to help bees return to the feeder once they have learned its location (Figure 1).

Figure 1. Honey bees foraging for 55% (w/v) sucrose solution on a grooved plate feeder

    b. Ensure that no more than 30 foragers visit the feeder at a time and remove bees with an aspirator as needed to reduce crowding.
4. To train bees, place a glass vial at the entrance of the nest to trap the bees flying out and bring them to a feeder 150 m away, where they are released and begin to imbibe sucrose.
    a. Individually mark the bees with different paint pen colors.
    b. Allow bees to visit the feeder a few times until they waggle dance.
    c. Continuously observe all visits of every bee to the feeder.
5. Record the first five waggle dance performances of five different bees per colony using a high-definition video camera (HDR-PJ790, Sony).
    a. Illuminate observation colonies with natural light from a window.
    b. Measure the time it takes for foragers to fly back from the feeder to the nest immediately before they waggle dance (defined as return times, with measurements coordinated with the hive and feeder observers via two-way radios).

C. Revisiting waggle dancing after 20 d of experience

1. Twenty days later, retrain the marked foragers whose first dances were observed to the same 150 m feeder locations and record their waggle dances to determine if their dancing has changed. At this point, the

workers should be, on average, 29 and 30 days old in experimental and control colonies, respectively. See Table 1 for a detailed description of bee type names.

Table 1. Definitions of the different colonies and bee types. The rationale explains the main reason for observing the dances at each stage.

Name	Definition	Rationale
Experimental colony	A single cohort colony created from bees that are all one day old.	Experimental colony
E1 naive first dances ($E1_{FD\ naive}$)	The first waggle dances performed by bees (9.0 ± 2.0 days old, mean ±1 standard deviation) in an experimental colony. They are *naive* because these bees could not follow other dances before performing their first dance.	What do the first dances of foragers that have never danced before or followed other dances look like?
E2 older dancers ($E2_{OD}$)	The waggle dances of E1 bees when they are 29 days old and have more experience following other dancers and dancing.	Do the dances of E1 bees change when they are 20 days older and have had experience dancing and following other dances?
Control colony	A multi-cohort colony consisting of bees of all ages.	Control colony
C1 first dances ($C1_{FD}$)	The first waggle dances performed by bees (9.9 ± 1.0 days old) in a control colony (control for E1).	What do the first dances of foragers that have never danced before but were able to follow other dancers look like?
C2 older dancers ($C2_{OD}$)	The waggle dances of C1 bees when they are 30 days old (control for E2).	Do the dances of C1 bees change when they are 20 days older and have had additional experience dancing and following other dances?

2. Video-record these waggle dancers and measure their return times (see above).
    a. Hypothesize that $E2_{Older\ Dancers}$ dances, due to experience, have increased precision and orderliness above that of $E1_{First\ Dances\ naive}$ dances.
    b. In the 20 days between $E1_{First\ Dances\ naive}$ and $E2_{Older\ Dancers}$ dances, the feeder is not available.
    c. Note that $E2_{Older\ Dancers}$ can only follow other dancers of the same age with similar experience levels. $C2_{Older\ Dancers}$ can follow dancers of different ages with different experience levels.

D. Measuring the waggle dance

1. To analyze the waggle dance, use Tracker software (V4.91).
2. Exclude the first waggle run for each dance of every bee and analyze the subsequent six waggle runs (Couvillon et al., 2012).
3. Define a dance as a series of consecutive waggle runs and return phases during one visit of a forager inside the nest.
4. For each dance (Figure 2), measure:
    a. The waggle run angle relative to gravity.
    b. The waggle dance divergence angle (the maximum difference between waggle angles during six waggle runs).
    c. The waggle run duration, defined from when the bee begins to turn and starts to waggle her abdomen to when she stops waggling her abdomen and moves into another turn.
    d. The waggle duration error (the duration difference between longest and shortest waggle run within a dance).
    e. Waggle duration variance (coefficient of variance of the waggle durations).
    f. The number of waggles per waggle run (each waggle is defined as one complete movement of the abdominal tip from right to left to right).

g. Variance in the number of waggles per waggle run (coefficient of variance of the number of waggles per waggle run per dance).
h. Return phase duration.
i. Return phase duration variance (coefficient of variance).
j. Total number of waggle runs within a dance.
k. The number of dance followers (each follower defined as a bee following a waggle dancer for ≥ 5 s) per waggle dance performance.
l. To measure the start and stop of a waggle run, respectively define them by measuring the start and stop of dancer wing oscillations from the video (recorded at 60 fps).
m. Measure the rate of return phase non-alternations (dance disorder) and define it as the number of non-alternating return phases (Tan et al., 2012).
   i. Count the pattern of consecutive return phases and calculate the disorder proportion by dividing the total number of return phase non-alternations by the total number of waggle runs within a dance.
   ii. After a dancer makes a waggle phase, she can make a return phase by turning either to her left (L) or her right (R). Dancers often alternate these return phases (i.e., L-R-L-R). A non-alternation return phase occurs when she makes two consecutive return phases in the same direction. For example, the pattern L-L-L-L would be counted as three return phase non-alternations, since we compare each return phase direction with the prior one.
n. For additional details on how to measure waggle dances, we recommend these excellent papers (Griffin et al., 2012; Preece and Beekman, 2014; Wario et al., 2015; Schürch et al., 2019).
o. Please see Video 1 and Video 2 for examples of waggle dances that show different levels of error.

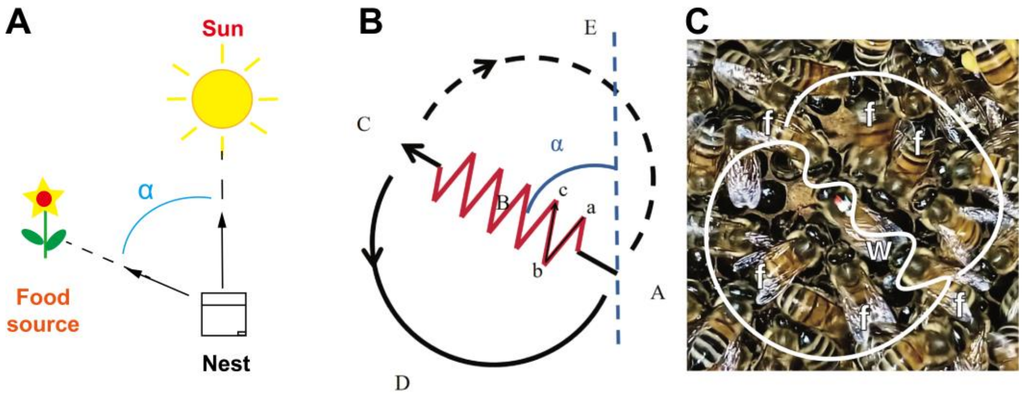


Figure 2. Diagram illustrating waggle dance measurements. The diagram on the left shows the location of the food source relative to the sun and the nest. This arrangement results in the waggle dance diagram shown in the center. In this diagram, the angle (α) of the waggle run is the angle between the waggle direction and the vertical dashed blue line (defined by gravity on a vertical comb). This waggle angle communicates the direction of the food source from the colony relative to the sun's azimuth at the time of the dance. For example, if a food source is in the direction of the sun, the waggle run points straight up. If a food source is in the direction opposite the sun, the waggle run points straight down. In this example, α = 45° to the left of the vertical line, and thus the food source is located 45° to the left of the sun's azimuth. The waggle run consists of waggling motions of the abdomen, made as the bee traverses a line crossing three points: A, B, and C. The waggle duration is measured from point A to point C. Each waggle is defined by the abdominal tip moving from points a-b-c. (one peak-to-peak cycle). The return phase duration is measured as the time it takes a bee to return from a completed waggle run, and is shown by the curve C-D-A or the curve C-E-A. In a fully ordered waggle dance, the dancer typically turns in the opposite direction on each repetition. For example, if the dancer traverses C-D-A, on the next return phase it will likely follow the path C-E-A. A photo of a waggle dancing bee (w) surrounded by dance followers (f) is shown for context on the right.

Data analysis

1. To analyze the data, use JMP Pro V16.1.0. You may also use different statistical software, but it is important to use repeated-measures models since you will be comparing the behavior of the same bees when they are younger and then older.
2. For testing the differences in age of first foraging between experimental and control colonies, use ANOVA with colony type as the independent variable and age of first foraging as the dependent variable.
3. For the measurements shown in Table 1, use Repeated Measures Mixed Models (REML algorithm) with colony type, bee ID, time point, the interaction of colony type × time point, and colony as random effects.
4. As needed, log-transform the waggle durations, waggle duration range errors, and the number of waggle runs based on the inspection of model residuals.
5. To test for differences between the treatment groups within a dance on variance in waggle durations, the number of waggles per waggle run, and return phase durations, calculate the coefficient of variation (CV = standard deviation/mean), and run the models with these coefficients of variation. Make all corrected pairwise comparisons using Tukey HSD tests.
6. To test for correlations between divergence angles and disorder proportions per dance, use linear regressions, one per bee type ($E1_{\text{First Dances naive}}$, $E2_{\text{Older Dancers}}$, $C1_{\text{First Dances}}$, and $C2_{\text{Older Dancers}}$, Table 1).

Validation of protocol

1. Data obtained by using this protocol can be found here: DOI: 10.5281/zenodo.7301648. The number of replicates recommended is shown in the datasheet provided.
2. Recommended statistical analyses are shown above.
3. These results were published in *Science* (2023), DOI: doi/10.1126/science.ade1702.

General notes and troubleshooting

Troubleshooting

Problem 1: It can be difficult to train bees to feeders some times of the year due to varying natural food availability.

Solution: Employ a classic, albeit slower, training technique by positioning the feeder in contact with the colony entrance. Note that this training method is not ideal for this experiment since we want to make sure to capture the first waggle dance of a bee. Thus, you will need to use only a low-concentration sugar solution that will still attract bees but for which they will not waggle dance.

1. Gradually increase the gap between the feeder and nest entrance in increments, first by moving it only 1 cm at a time and later by meters once bees commence flying to the feeder (Seeley, 1995).
2. Ensure all trained bees return before relocating the feeder.
3. If bees fail to return, revert to the feeder's previous position, and decrease the relocation distance.
4. Maintain a record of bees visiting the feeder using a census sheet each 15 min or at shorter regular time intervals, as determined by the rate at which you are moving the feeder. Recording bee visitation helps to ensure that your bees are continuing to visit as you move the feeder.
5. Once bees are at the final location, increase the sugar solution concentration to elicit waggle dancing.

Problem 2: Bees do not consistently perform waggle dances.

Solution: Select a period of relative natural food scarcity.

1. Increase sucrose concentration if consistent waggle dancing remains unobserved.

2. Utilize a saturated sucrose solution (2.5 M) if needed.
3. If waggle dances persistently fail to materialize, consider rescheduling experiments for a different time of the year.

Problem 3: During periods of food dearth, non-focal colonies discover the feeder and compete with trained bees.

Solution: Implement the following preventative measures:
1. Rigorously monitor training. Mark each bee that lands on the feeder and verify its return to the focal colony. If the marked bee is absent from the focal colony, capture it with an aspirator and freeze it at day's end upon its subsequent return to the feeder. This minimizes bee sacrifice by curbing recruitment from non-focal colonies.
    a. To freeze bees, it is simplest to have multiple aspirators.
    b. Place the aspirator with the captured bees inside a freezer at -20 °C for at least 12 h to sacrifice them.
2. Refrain from training bees at previously used locations visited by non-focal bees.
3. Minimize sucrose concentration to limit recruitment, as higher concentrations increase recruitment. Employing the minimum concentration necessary for trained foragers to revisit the feeder mitigates the risk of massive recruitment by non-focal colonies and regulates focal colony forager numbers. Once you have established the feeder at the correct final location, you can then use a higher sucrose concentration to elicit waggle dancing by the bees.
4. Recognize that the observation colony has fewer combs than standard and feral colonies, making it easier for non-focal colonies to overtake the feeder.
5. If feasible, conduct experiments in areas with fewer competing honey bee colonies.

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This protocol was derived from the original work of Dong et al. (2023).

Competing interests

The authors declare no competing interests.

Ethical considerations

We used honey bees, *Apis mellifera*, which are invertebrates that are not endangered or protected and do not require Institutional Animal Care and Use Committee protocol authorization.

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