COMPLEMENTARY SESSION PAPER

Foraging Under Fire: A Robotic Flower System Incorporating Multimodal Signaling and Aversive Stimuli

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Synopsis Artificial flowers have long been used in pollinator research to understand and manipulate key floral features such as rewards and display. Increased access to 3D printing and Internet of Things (IoT) technologies has expanded the capabilities of artificial flowers, enabling more precise control and real-time data collection. These IoT-enabled artificial flowers, referred to as robotic flowers or robo-flowers, integrate single-board computers, such as the Raspberry Pi series or similar embedded system devices, as well as affordable camera and sensor modules. However, despite their flexibility and modularity, the majority of robotic flowers are designed to investigate how pollinators make foraging decisions based on visual cues linked to floral rewards, with less attention paid to the broader information landscape that pollinators use to decide which flowers to visit. We have developed a robotic flower system that extends this approach to incorporate multimodal signaling capabilities as well as aversive floral stimuli. These stimuli were designed to allow for investigation into the more nuanced information tradeoffs that feature in pollinators foraging decisions, but the designs could be broadly useful for researchers interested in understanding insect nociception, decision-making, and apparent predation in the context of plant–pollinator interactions.

Introduction

Pollinators face a series of tough decisions in the floral market. They must process and integrate a complex medley of cues, stimuli, and rewards to decide which flowers and flower patches to visit (Chittka et al. 1999), how long to spend on each flower and patch (Mustajrvi et al. 2001), and how to maximize energetic and nutritional payoff from their foraging efforts (Foster et al. 2014; Russell et al. 2016). In addition to integrating information about the relative nutritional quality among flowers, pollinators must consider floral visitation history (Forster et al. 2023), floral handling times, and even predation risk (Chittka et al. 1999; Jones and Dornhaus 2011; Fragoso and Brunet 2023). Pollinating bees have long been used to study how pollinators interpret the varied and sometimes conflicting lines of information being broadcast by flowers, and a growing interest among researchers in insects as sentient beings with the ability to have subjective experiences (Klein and Barron 2016), feel pain (Gibbons et al. 2024), and even play (Galpayage Dona et al. 2022), sets the stage for deeper exploration into the decision-making processes of individual bees. However, investigating the salience of specific floral cues in the context of pollinator preference and decision-making is challenging in most natural environments, such that it has become common practice to use simplified artificial flower models for conducting pollinator behavioral assays under controlled laboratory settings.

Artificial flowers have been employed to study pollinator decision-making for many decades. Some of the simplest designs are little more than cups containing sugar rewards, such as Grossmann's (1973) early designs to study how different positive reinforcement strategies affect honey bee behavior. Other designs have investigated memory retention in bumble bees (Keasar et al. 1996), the effects of non-rewarding flowers on individual bees' foraging behavior (Keasar 2000), the relative importance of pollen and nectar in attracting pollinators, and patch departure behavior (Essenberg 2015).

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The majority of previous artificial flower designs focused their designs on attractant floral features like visual cues, though a few notable exceptions have sought to incorporate negative stimuli such as heat (Gibbons et al. 2022) or simulated predator threat (Ings and Chittka 2008) to understand the role of negative stimuli in pollinator decision-making. These previous designs have all contributed fundamental insight into the multiple cues that underlie complex decision-making processes in pollinating bees. Yet, whether due to researcher interest or technical constraints, many existing tools rely on highly simplified designs that incorporate a limited range of sensory modalities, rewards, and stimuli into the floral design, and, critically, rely on human observers to record visitation data, thereby limiting the spatial and temporal scales at which experiments can be

We present a robotic flower system that incorporates automatic data capture with multiple modes of floral signaling (i.e., visual and olfactory signals), positive stimuli in the form of liquid reward (artificial nectar), and aversive stimuli in the form of noxious heat or a mock floral predator. Our design integrates and extends several elements from previous robotic flower systems (Ings and Chittka 2008; Kuusela and Lms 2016; Gibbons et al. 2022; Debeuckelaere et al. 2024) developed specifically for large-bodied bees, as these are commonly studied pollinators in lab-based behavioral assays (Lihoreau et al. 2025, and references therein). We present several additions that improve experimental options, and we discuss possible extensions and modifications that could be employed across a broad range of research questions related to pollinator decision-making and foraging behavior. The resulting robotic flower system provides a highly customizable, inexpensive, and accessible means of investigating a broader range of the rich information landscape that pollinators must navigate.

Robotic flower design Basic design elements

The robotic flowers (Fig. 1) consist of a hollow "stem" fitted with a floral "display" with a detachable camera stalk, all designed in Autodesk Fusion 360 version 2.0.20970. These components were printed on Raise 3D N2 and Creality K1C FDM 3D printers using polylactide (PLA), a widely utilized biopolymer known for its affordability, biodegradability, and ease of processing. As a 3D printing filament, PLA exhibits strong layer adhesion at relatively low temperatures, making it printable on even entry grade 3D printers. This makes it one of the most commonly used materials, while being available in a wide variety of colors. These properties, coupled with various design elements enable simple and

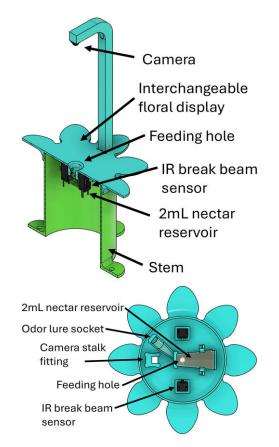


Fig. 1 Main components of the robotic flower design. Top: cross section of the flower's external and internal components. Bottom: the underside of the floral display showing elements mounted below.

consistent assembly or part replacement within the apparatus. At the bottom of the stem are four screw holes for mounting to a flat surface of the experimental arena. A full hardware and equipment list is available at the project's GitHub page at https://github.com/Whitaker-Lab/Robo-Flowers.

The camera stalk is printed in the same color as the corresponding floral display, and the stalk design file can be parametrically adjusted to print at different heights to control the camera's field of view. The stalk shape was designed to accommodate a small USB camera (Adafruit #5733) pointed downward toward the center of the floral display, where the feeding hole is located. Because we designed the robotic flowers for experiments using common eastern bumblebees (Bombus impatiens), the feeding hole is 1 mm deep and 3 mm in diameter, recessed in a cavity 14 mm long and 10 mm wide such that only a single bumblebee worker can feed at a time. When a bee enters the feeding hole, its body physically interrupts an infrared beam (IR) being transmitted across the feeling hole by an IR break beam sensor, which is mounted immediately below the feeding hole on the underside of the floral display (Fig. 1). The broken beam triggers a single-board computer (Raspberry Pi Zero WH) to record the time and duration of the interruption, such that feeding events are recorded automatically. This approach is commonly used in other robotic flower systems (Sokolowski and Abramson 2010; Kuusela and Lms 2016; Debeuckelaere et al. 2024) and operates under the assumption that time spent in the feeding hole can be interpreted as time spent actively feeding.

If the bees are marked or tagged (for example, with ARUCO tags or similar QR-based IDs), images taken by the overhead camera can be used to associate individual bees with their respective feeding events, a particularly useful feature if the experimental design calls for multiple bees foraging in groups. At 640×680 pixels, these cameras are sufficient for basic picture-taking and some light-weight machine vision projects, but higher quality optics may be necessary depending on the intended use (see the "Extensions and modifications" section).

The camera and IR break beam sensor are controlled by the same Raspberry Pi Zero WH single-board computer connected beneath each floral display and mounted on the underside of the foraging arena. Each Raspberry Pi Zero WH is capable of operating the camera and IR break beam sensor simultaneously while also capturing image and visitation data to be saved locally and/or transmitted to another networked device.

Finally, mounted at the base of the feeding hole is a nectar reservoir printed from a clear and biocompatible (ISO-10,993 certified) UV resin printed on an Elegoo Saturn 8k resin 3D printer. The nectar cups were designed with a 5 mm threaded fitting to enable potential automatic refilling and easy washing. Because our experimental design did not require nectar reservoirs to self-refill, the nectar cups were designed with a maximum internal capacity of 2.69 mL, a volume that far exceeds the amount that a single bee can consume at a time (\sim 105 [Pattrick et al. 2020]). For experiments in which groups of bees are allowed to forage freely for extended periods, 2 mL was, therefore, more than sufficient and allowed for long experimental periods without needing to refresh artificial nectar. The shape of the internal cavity of the reservoir is such that the liquid inside gravity feeds to the lowest spot within the reservoir, which we design to be oriented within range of a bee's tongue of up to 8 mm (Cariveau et al. 2016). This design allows a bee to feed on the artificial nectar even if the reservoir is filled with smaller volumes or is almost empty. The nectar cups are reusable and are washed with soap and water between uses. A drain hole on the side of the reservoir is used to empty excess nectar, but it is physically plugged during experiments to prevent leaking.

Multimodal signals

For a two-choice experiment with common eastern bumblebees (*B. impatiens*), we printed blue and yellow floral displays based on previous studies demonstrating that bumblebees can see and discriminate between these colors (Wolf and Chittka 2016; Zhou et al. 2020), leading to their common use in two-choice assays with bees (Smithson and Macnair 1996; Raine and Chittka 2008).

In addition to these visual signals, we also integrated an olfactory signal into the design. Target volatile organic compounds (VOCs) are suspended in paraffin oil and placed on strips of filter paper placed inside a 1 mL pipette tip, sealed with laboratory film at the large end. The pipette tip fits in the floral display with the small opening pointing directly at the feeding hole, emitting an olfactory signal as the VOC passively evaporates from the pipette tip into the feeding hole. If more control is needed over the evaporation or emission rate, controlled air flow could be easily added to this component (see the "Extensions and modifications" section). We found that including an attractant floral odor (e.g., methyl salicylate) greatly improved the time it takes bees to learn to visit and feed from the flowers, but any volatile signal could be presumably used in the odor lures, including aversive odors, to test pollinator responses to olfactory signals alone or in combination with other floral signals.

If other airborne emissions are desired, such as humidity or CO₂, the odor lures could be easily adapted to do so, and the position of the lure(s) can be moved to other locations of the floral display if spatial distribution is of interest (see the "Extensions and modifications" section).

Aversive stimuli

Whereas colors and scents can be attractant, deterrent, or neutral to pollinators, we intended to incorporate distinctly aversive stimuli into our floral design to allow controlled study of the role of negative stimuli in pollinator decision-making. Aversive stimuli are an important but often understudied component of pollinator decision-making, and we currently use this setup to study pollinator motivation for floral rewards by measuring bees willingness to tolerate uncomfortable, painful, or threatening experiences to receive a given floral reward.

Noxious heat has been used as an aversive stimuli in pollinator decision assays before (Gibbons et al. 2022). This allows us to leverage heat as negative stimuli to better understand how bees make foraging decisions when faced with physically detrimental inputs in light of not nutritional rewards. Building off a design by Gibbons et

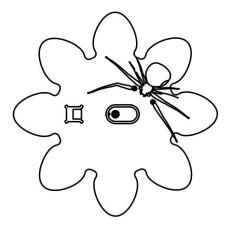


Fig. 2 Spider predation system designed to emulate a goldenrod crab spider (*M. vatia*).

al. (2022), we implemented a heating element into the feeding hole comprised of a piece of nichrome foil encased between two pieces of Kapton tape. The foil can be heated to a desired temperature by a HiLetgo DC 3-5V MAX6675 Module + K Type thermocouple temperature sensor controlled by the Raspberry Pi. This system uses pulse-width modulation to keep the temperature of the heat pad at the desired temperature (e.g., 55°C). Although noxious heat is not a floral stimulus that pollinators would encounter under realistic natural conditions, it is a simple and useful useful approach for measuring insects' willingness to tolerate physical pain or discomfort in pursuit of floral reward.

For a more realistic scenario, we developed a mock floral predator that can be mounted on the floral display adjacent to the feeding hole (Fig. 2). Our mock predator is modeled after the goldenrod crab spider (Misumena vatia), a common floral ambush predator of pollinating bees. Due to its small size, the mock predator is printed using a resin 3D printer from the same clear resin as the nectar reservoirs. This provides a degree of crypsis to the model, though further testing is needed to verify this. The mock predator is equipped with movable pinching "arms" controlled by a SG90 micro servo. In an open position, these "arms" are positioned around the feeding hole, and are triggered by a landing bee to slowly close around the feeding hole, pinching the visiting bee. Videos of this behavior can be found on the project's GitHub page. The motion is triggered by a pressure sensor connected to a Hemobllo strain gauge. The sensors and micro servomotors controlling the spider are allocated to an Arduino Nano with built-in analog-todigital converters (ADCs), enabling quick response to capture signals from the strain gauge while preventing potential latency from non-real-time tasks occurring on the Raspberry Pi. Apparent predation in the context of plant-pollinator interactions has received less

study than other plant-herbivore interactions, such that the approach described here may benefit future investigation into the roles of non-consumptive effects and predator threat in pollinator foraging decision-making.

Importantly, not all of the features and stimuli described here need to be incorporated at once. Researchers can (and should!) select the features most important for their research question, omit unnecessary signals and stimuli, and aim to mix and match according to their experimental goals.

Internet of things deployment

We currently employ 20 robotic flowers that are each controlled by an individual Raspberry Pi Zero WH, all of which are centrally managed by a single Raspberry Pi 5 through wifi. This Internet of Things (IoT) system architecture allows us to run the Raspberry Pi OS Lite operating system on the Raspberry Pis controlling flowers ("flower Pis"), which does not include a desktop and thereby reduces the total disk space required for the operating system. We then run the flower Pis in headless mode (i.e., without a computer screen or peripherals), accessed from the command line on a Raspberry Pi 5 ("central Pi"). The central Pi runs the full Raspberry Pi OS with desktop, and it is connected to a large computer screen, mouse, and keyboard, such that it can be operated like a normal desktop computer.

To run an experiment, scripts are pushed from the central pi to the flower Pis and executed in sequence, with only a short delay (a few seconds) across flower Pis depending on network speed. If scripts need to start on every flower Pi at precisely the same time, only slight modification would be needed to the code to push the scripts in sequence but execute them at a specified start time. At the end of an experiment, the central pi fetches the data and images collected from each flower Pi, and the files can then be downloaded to personal computers via WiFi for analysis. The central Pi also saves the fetched data files to an external hard drive for additional backup. The system architecture is shown in Fig. 3.

Discussion

We aimed to develop a robotic flower system that is modular, highly flexible, and durable. In two-choice assays in which small groups of bumblebees (*B. impatiens*) were allowed to forage freely from the robotic flowers provisioning 1.5M sucrose solution, the flowers recorded feeding events continuously over 5 days (Fig. 4) without requiring the artificial nectar to be refreshed (or any other human intervention).

In developing our flower system, we drew from many of the existing designs of artificial and robotic flowers but extended the designs to include both multi-modal

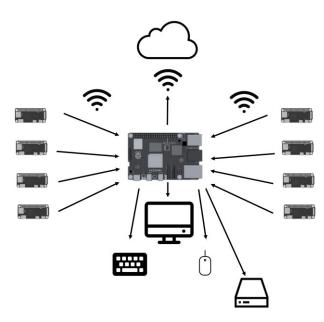


Fig. 3 System architecture of the networked Raspberry Pis. Raspberry Pi Zero WH SBCs are run in headless mode and managed via WiFi by a central Raspberry Pi 5 connected to desktop peripherals. Data are accessed through WiFi and are also backed up on an external hard drive connected to the central pi.

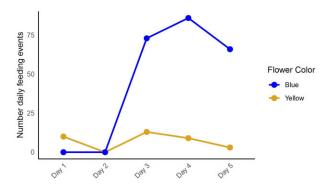


Fig. 4 Number of daily feeding events by *B. impatiens* foragers over 5 days of continuous access to the robotic flowers conveys an innate color preference for blue flowers, as has been shown previously.

signaling capabilities and aversive stimuli. Multi-modal floral signaling has been shown to be highly relevant in the context of pollinator foraging decisions (Kulahci et al. 2008; Leonard and Masek 2014). Because artificial flower systems provide the ability to control specific floral features that may not be possible to manipulate under natural conditions, they are uniquely suited to testing different *combinations* of floral features. However, despite the growing availability of 3D printed artificial and robotic flower systems, very few systems explicitly incorporate multiple sensory modalities into their designs (but see Chapman et al. [2023]), such that our adaptable approach will hopefully contribute to future

investigations into multi-modal signaling in pollinator decision-making.

Moreover, artificial flower systems that incorporate aversive stimuli are generally less diverse than the plethora of systems that feature floral rewards alone. Aversive stimuli are known to be critically important in pollinator decision-making, but the role of apparent predation is relatively understudied in the context of plant–pollinator interactions. While investigations in nature are needed, the robotic flower system presented here provides a novel resource for mixing and matching aversive stimuli with other floral features.

Nevertheless, there are a few caveats and risks to implementing the robotic flower system that should be considered. The biggest potential risk inherent in using any artificial flower system, but perhaps especially robotic or otherwise "high tech" designs, is that the design features may drive the research questions, rather than the other way around. Indeed, many important insights about pollinator decision-making have been borne from experiments using much simpler, "lowtech" artificial flower setups. One of the biggest advantages of using a robotic flower system such as ours is the option for automated data capture that would otherwise be infeasible using human observers. If the perceived benefits of using a robotic flower system outweigh the costs, it is important to carefully consider the study's motivation, hypotheses, and experimental design when choosing which floral features to include and manipulate. Our aim is to present an experimental resource that enables previously intractable research questions, not to create a scenario in which technology constrains discovery.

One should also consider the workload and learning curve required to build and operate robotic flowers versus analog artificial flower designs. Construction requires access to specialized tools and equipment, though most universities possess multiple 3D printers, and the majority of hardware and electronic components are readily available through online stores targeting makers and hobbyists. Working with SBCs comes with a steep learning curve for new users, though there are myriad user-friendly help guides and tutorials online for programming and troubleshooting Raspberry Pis, and we have found students with no previous coding background have been able to quickly learn to operate and manage the Pis. Finally, while the robotic flowers are relatively inexpensive on a per-unit basis, project budgets can quickly balloon as a project scales, and if higher quality cameras are needed, this could significantly increase total costs.

In designing, implementing, and testing our robotic flower system within the context of a research laboratory at a public university, the biggest challenge we

faced was troubleshooting reliable access to our university WiFi network. Many university networks are hesitant to implement IoT setups due to security concerns, so it is important to coordinate with institutional network administrators early and throughout the project. Some network administrators might be willing to create a project-specific sub-network, and others might be willing to assign static IP addresses to prevent the devices from getting disconnected from the network as traffic increases. To circumvent these issues entirely, researchers may wish to implement a private network for the robotic flowers, which would offer added flexibility in terms of experimental location, perhaps moving to a greenhouse or semi-natural enclosure. While our design was developed for indoor experiments, Debeuckelaere et al. (2024) have developed a robotic flower system for large-scale data capture in natural settings, such that elements from both systems could be integrated to bring experiments outdoors.

Extensions and modifications

Given the growing access to 3D printing equipment and the widespread availability of inexpensive off-the-shelf sensors and controllers, many options exist for future experimental applications and modifications. However, we suggest dedicating ample time to designing and testing any extensions or modifications. We have found design and construction to be highly iterative processes, and some of our best ideas have been rendered moot by the unanticipated behavioral quirks of our study organisms. Here, we discuss potential extensions that may be desirable to other researchers, along with our suggested approach.

Flower shape is an important floral feature for pollinators, such that some researchers may wish to modify the shape of the floral display, which is easily accomplished in Autodesk or other 3D modeling software. It may also be desirable to create flowers with multiple colors and patterns, though this would be difficult to do from purely 3D printed elements unless researchers were willing to conduct some more sophisticated assembly. An alternative approach would be to choose a printing material that could be easily recolored with ink or paint, taking care to check the spectral properties to ensure visibility to insects. Inexpensive UV paint markers could be used to add nectar guides around the feeding hole or additional markings and patterns to the floral displays.

The size of the flowers can also be rescaled to be larger or smaller, taking care to keep the size of the necessary floral elements (e.g., IR sensors, nectar cup, etc.) constant, or resizing all elements if the experiment calls for it. If the floral display is resized, the stem should also be resized to ensure a tight fit between the two components, as we have observed some bees trying to access the nectar cup from the underside of the floral display, as if attempting to nectar rob. Furthermore, the distance between the IR sensors should be kept constant (or tested for accuracy, if modified), as the sensitivity of the sensors is greatly impacted by the distance between them

Other possible modifications include the addition of a pollen-dispensing element or implementing an automated refilling nectar cup. The pollen-dispensing element could be as simple as a chenille pipe cleaner wrapped around the camera stalk or installed elsewhere on the display surface, similar to Russell and Papaj (2016) and Chapman et al. (2023), or as complex as installing a fine-tuned strain gauge to monitor pollen collection by weight. If self-refilling nectar cups are needed, the drain hole could be repurposed as an attachment point for a refilling system.

If computer vision capabilities or other machine learning algorithms requiring a higher degree of visual fidelity are going to be implemented into the system, a higher quality camera module will likely be necessary. There are many Raspberry Pi-compatible cameras available with a broad range of optical quality and capabilities. Many camera modules use an AV ribbon to connect to the Raspberry Pi instead of a USB cable, which would require slight modification to the camera stalk.

Researchers may also be interested in modifying the odor lure to add functionality for controlling air flow rates or testing other sensory modalities, such as relative humidity, CO_2 , or air temperature. Tubing could be attached to the large end of the pipette tip to connect the lure to a source of controlled air flow, requiring only a slight change to the odor lure fitting. In the present design, the odor lure requires a relatively large footprint on the underside of the display, but this could be resized or moved to the stem if the space is needed for tubing or for additional sensors or components. Alternatively, the odor lure socket could be scaled down to accommodate a smaller pipette tip.

Finally, the mock predator could be replaced with other mock organisms that are relevant in plant-pollinator or pollinator-pollinator interactions. For example, mock conspecific or heterospecific bees could be used to quantify the importance of pollinator competition or interspecific and intraspecific cues. The mechanics used to drive the motion of the mock predator could be repurposed to control other mock organisms if motion remains a desirable feature. The strain gauges used to trigger motion in the mock predator are fairly fragile and can break if not handled carefully. If a more robust (albeit less precise) motion trigger is needed, a

small motion sensor could be used instead of a strain gauge.

Tips for success

In addition to devoting ample time to testing the system's overall operability, we recommend doing regular checks of the sensors and network connectivity before every experiment. Depending on network stability, the Raspberry Pis may need to be restarted if they get dropped from the network. Because the flower Pis are run in headless mode, having a portable Raspberry Picompatible touchscreen handy can be very useful when troubleshooting network connectivity issues.

Users should also be aware that the infrared break beam sensors can be quite sensitive, and, depending on the diameter of the feeding hole and the distance between the sensors, the infrared beam can reflect off the surface of the feeding hole when a bee enters, introducing substantial noise into the raw visitation data. Adding resistors into the wired connection from the sensors to the Raspberry Pi is one option for using hardware to reduce the sensitivity, but we chose to instead deal with the noisy data by applying aggregating functions to the raw data. We recommend establishing a minimum threshold for the time required to constitute a feeding event, as well as the time between beam breaks to count as distinct feeding events.

Similarly, users may want to apply maximum time limits for feeding events, especially if the large-capacity nectar cups are used. We have occasionally observed bees asleep inside the feeding holes of the flowers, resulting in a continuous break in the IR beam and unrealistically long feeding events recorded in the raw data.

Author contributions

J.F., S.M. D.Z, and M.R.L.W conceived the flower design and experiments; J.F. and D.Z constructed the 3D printed and electronic elements; S.M. conducted the validation experiments, M.R.L.W wrote the operating code. J.F. and M.R.L.W wrote the initial draft of the manuscript, with input provided from all authors.

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Data availability

All information required to recreate and modify the robotic flower systems, including 3D printing design files (.stl), operating code, hardware lists, and photographs and videos of bumble bees interacting with the robo-flowers, is freely available from the project's GitHub page (https://github.com/Whitaker-Lab/Robo-Flowers).

References

- Cariveau DP, Nayak GK, Bartomeus I, Zientek J, Ascher JS, Gibbs J, Winfree R. 2016. The allometry of bee proboscis length and its uses in ecology. PLoS One 11:e0151482.
- Chapman KM, Richardson FJ, Forster CY, Middleton EJT, White TE, Burke PF, Latty T. 2023. Artificial flowers as a tool for investigating multimodal flower choice in wild insects. Ecol Evol 13:e10687E10687. https://onlinelibrary.wiley.com/doi/pd f/10.1002/ece3.10687
- Chittka L, Thomson JD, Waser NM. 1999. Flower constancy, insect psychology, and plant evolution. Naturwissenschaften 86:361–77.
- Debeuckelaere K, Janssens D, Serral Asensio E, Wenseleers T, Jacquemyn H, Pozo MI. 2024. A wireless, remotely operable and easily customizable robotic flower system. Methods Ecol Evol 15:1312–24.
- Essenberg CJ. 2015. Flobots: robotic flowers for bee behaviour experiments. J Pollination Ecol 15:1–5.
- Forster C, Middleton E, Gloag R, Hochuli D, White T, Latty T. 2023. Impact of empty flowers on foraging choice and movement within floral patches by the honey bee, apis mellifera. Insectes Soc 70:413–22.
- Foster JJ, Sharkey CR, Gaworska AV, Roberts NW, Whitney HM, Partridge JC. 2014. Bumblebees learn polarization patterns. Curr Biol 24:1415–20.
- Fragoso FP, Brunet J. 2023. Honey bees exhibit greater patch fidelity than bumble bees when foraging in a common environment. Ecosphere 14:e4606.
- Galpayage Dona HS, Solvi C, Kowalewska A, Mkel K, MaBouDi H, Chittka L. 2022. Do bumble bees play? Anim Behav 194:239–51.
- Gibbons M, Pasquini E, Kowalewska A, Read E, Gibson S, Crump A, Solvi C, Versace E, Chittka L. 2024. Noxious stimulation induces self-protective behavior in bumblebees. iScience 27:110440.
- Gibbons M, Versace E, Crump A, Baran B, Chittka L. 2022. Motivational trade-offs and modulation of nociception in bumblebees. Proc Natl Acad Sci 119:e2205821119.
- Grossmann KE. 1973. Continuous, fixed-ratio, and fixed-interval reinforcement in honey bees. J Exp Anal Behav 20:105–9.
- Ings TC, Chittka L. 2008. Speed-accuracy tradeoffs and false alarms in bee responses to cryptic predators. Curr Biol 18:1520-4.
- Jones EI, Dornhaus A. 2011. Predation risk makes bees reject rewarding flowers and reduce foraging activity. Behav Ecol Sociobiol 65:1505–11.
- Keasar T. 2000. The spatial distribution of nonrewarding artificial flowers affects pollinator attraction. Anim Behav 60:639–46.

Keasar T, Motro U, Shur Y, Shmida A. 1996. Overnight memory retention of foraging skills by bumblebees is imperfect. Anim Behav 52:95–104.

- Klein C, Barron AB. 2016. Insects have the capacity for subjective experience. Anim Sentience 1: 1–19
- Kulahci IG, Dornhaus A, Papaj DR. 2008. Multimodal signals enhance decision-making in foraging bumble-bees. Proc R Soc B Biol Sci 275:797–802.
- Kuusela E, Lms J. 2016. A lowcost, computercontrolled robotic flower system for behavioral experiments. Ecol Evol 6:2594– 600.
- Leonard AS, Masek P. 2014. Multisensory integration of colors and scents: insights from bees and flowers. J Comp Physiol A 200:463–74.
- Lihoreau M, Monchanin C, Lacombrade M, Brebner J, Gmez-Moracho T. 2025. Why bumblebees have become model species in apidology: a brief history and perspectives. Apidologie. 56:19.
- Mustajrvi K, Siikamki P, Rytknen S, Lammi A. 2001. Consequences of plant population size and density for plantpollinator interactions and plant performance. J Ecol 89:80–7.
- Pattrick JG, Symington HA, Federle W, Glover BJ. 2020. The mechanics of nectar offloading in the bumblebee *Bombus terrestris* and implications for optimal concentrations during nectar foraging. J R Soc Interface 17:20190632.

- Raine NE, Chittka L. 2008. The correlation of learning speed and natural foraging success in bumble-bees. Proc R Soc B Biol Sci 275:803–8.
- Russell AL, Golden RE, Leonard AS, Papaj DR. 2016. Bees learn preferences for plant species that offer only pollen as a reward. Behav Ecol 27:731–40.
- Russell AL, Papaj DR. 2016. Artificial pollen dispensing flowers and feeders for bee behaviour experiments. J Pollin Ecol 18:13–22.
- Smithson A, Macnair MR. 1996. Frequencydependent selection by pollinators: mechanisms and consequences with regard to behaviour of bumblebees *Bombus terrestris* (L.) (Hymenoptera: apidae). J Evol Biol 9: 571–88.
- Sokolowski MB, Abramson CI. 2010. From foraging to operant conditioning: a new computer-controlled Skinner box to study free-flying nectar gathering behavior in bees. J Neurosci Methods 188:235–42.
- Wolf S, Chittka L. 2016. Male bumblebees, Bombus terrestris, perform equally well as workers in a serial colour-learning task. Anim Behav 111:147–55.
- Zhou Y, Sun L, Peng X, Solvi C, Peng F. 2020. Chromatic, achromatic and bimodal negative patterning discrimination by free-flying bumble bees. Anim Behav 169: 93–101.